School of Environmental Biology

Ecology of *Eucalyptus victrix* in grassland in the floodplain of the Fortescue River

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DECLARATION

I declare that all work presented in this thesis is that of myself alone unless otherwise acknowledged. The contents of this thesis have not been submitted previously, in whole or in part, in respect of any other academic award.

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ABSTRACT

The WA coolibah tree, *Eucalyptus victrix* L. Johnson & K. Hill forms an unique and pristine woodland in the Fortescue Valley, in the Pilbara district of Western Australia. Until recently, no research had been done on *E. victrix* ecology and concern had been expressed by pastoral managers and others about the condition of the woodland occupied by this species. This research was an attempt to understand the ecology of coolibah using a multi-disciplinary approach.

A population demographic study of stands in *E. victrix* woodland reveals that the present tree populations occupy larger areas than saplings and seedlings. Soil moisture and warm summer temperatures are believed to be stimulating factors for seedling recruitment of *E. victrix*. Different size classes (height/diameter) reflect different recruitment events and these reflect past availability of seeds and adequate soil moisture in that particular area of the woodland. Occasional grasshopper outbreaks and drought cause canopy shrinkage. Presence of hollow boles, restrict dendrochronological examination of tree ages.

An important population study was of a post-seedling cohort at Roy Hill, where height distribution reflected a typical single recruitment event. In subsequent years (1995 - 1998) height measurement showed several peaks, suggesting that seedlings were now growing at different rates. Uniform and steady height growth was observed on saplings found at the edges of gilgai. During May 1998 several saplings flowered, it was assumed that *E. victrix* attained its reproductive maturity at mean height of 2.50 m and with a stem diameter of 50 mm.

Seedling recruitment and subsequent growth mainly depend on heavy rainfall or flooding events. Seedling recruitment occurs only from current seed rain. Seed longevity reduces after 54 days of burial at 50 mm depth. Mortality (4 - 6 leaf stage) of newly recruited seedlings during subsequent dry months is very high. Furthermore, allelopathic effects (root competition from established grass and insect herbivory) are additional causes of seedling mortality in the years of recruitment.

Seedlings recruited at a burnt (disturbed) site, grew faster compared with undisturbed sites with less mortality. This suggested that fire created a suitable condition by reducing root competition, increasing soil nutrients and also creating a gap which providing sufficient solar radiation for seedlings to establish and develop into a healthy population. It is suggested that once newly recruited seedlings overcome the first summer, mortality rates during subsequent years are drastically reduced.

Long-term waterlogging of *E. victrix* seedlings significantly increases seedling stem diameter. Large numbers of adventitious roots are developed and lenticels proliferate on the submerged portion of the stem. Flooding reduces each of photosynthesis, transpiration and stomatal conductance. Flooding does not increase shoot fresh or dry weight on 4-, 8- or 17- week old seedlings. Leaf emergence may be stimulated on flooded seedlings compared with unflooded seedlings. While root dry weight is greater in 17- week old flooded plants than on 13 - week seedlings, this difference is not significant. It is suggested that maintenance of a high root/shoot ratio is a drought adaptation. Furthermore, a comparative study of flood tolerance in semi-arid eucalypt species suggests that those species intolerant of flooding seldom express morphological adaptations and fail to recover from physiological damage.

The annual grass *Setaria dielsii* occurs under the canopy of mature *E.victrix* trees of the coolibah woodland. This species has probably displaced more palatable perennial grasses. Soil moisture under trees is slightly higher and soil temperatures are less extreme than away from the canopy. Growth of *S. dielsii* appears to be more associated with soil nutrient status. Levels of total N, Mg, K, S and of electrical conductivity (EC) under trees are significantly higher than those away from the tree. Levels of Ca, Na, Fe, and organic carbon do not differ. The under story sub-shrub *Malvastrum americanum* is an important competitor with *S. dielsii*. Light availability may determine relative biomass contributions of these two species.

The effect of the density of grass species, growing space and time of establishment on *E. victrix* seedlings (inter-specific competition), and the effect of density and growing space within *E. victrix* seedling populations (intra-specific competition) were studied under controlled conditions. Results indicate resources necessary for growth of individual *E. victrix* seedlings were more limiting under increased density of neighbouring grass species than under intra-specific competition. In particular photosynthetic area was drastically reduced in mixed culture.

Lack of ground cover beneath the canopy of isolated *E. victrix* trees was ascribed to toxic or phenolic substances present in leaf, bark and leaf litter of *E. victrix*. *Lactuca sativa* seed germination subjected to extracts and leachate demonstrated that the fresh leaf of *E. victrix* possesses toxic substances which cause deleterious effects on both germination and radicle development. Similarly, increasing concentrations of leaf and bark leachate show reduced germination percentage of *L. sativa* seeds. Shoot and root biomass of grass and eucalyptus treated with leaf leachate were reduced. *E. victrix* leaf leachate significantly reduced shoot and root biomass of its own seedlings. High Performance Liquid Chromatogram (HPLC) analysis separated 11 and 8 possible toxic substances from leaf and bark extracts respectively.

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DEDICATION

This thesis is dedicated to my postgraduate lecturer, the late, Prof. S. Balasubramaniam, a very special person in my life, who introduced me to Forest Ecology.

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CHAPTER 1

General introduction

Introduction

This chapter presents, a general introduction to the target species. A description is provided of its taxonomic status, habit and distribution in the study area. The study area is also described in terms of rainfall, soil, associated vegetation and land use.

The coolibah species *Eucalyptus victrix* L. Johnson and K. Hill, occurs naturally in woodlands on the floodplain of the Fortescue River north of Newman in the Pilbara District of Western Australia. Until recently little was known of the ecology of this species. The scope of the current research was to examine and explain the distribution and population dynamics of *E. victrix* in coolibah woodland. Flooding tolerance, adaptation to waterlogged conditions, competition between *E. victrix* seedlings and grass species, possible allelopathic effects on herbage, seed viability, leaf longevity, and grasshopper damage are important aspects of this study.

Taxonomic status

E. victrix was previously known as *Eucalyptus microtheca* F. Muell. The name change resulted from a recent revision of the taxonomic status of those species of Eucalyptus known as 'coolibah' (Hill and Johnson 1994).

The first species formally named within the group generally known as 'coolibah' was *Eucalyptus microtheca,* described in 1863 by Mueller (Hill and Johnson 1994). The same species was recognised by Bentham (1867) and by Maiden (1903-33). Blakely (1965) was the first to divide the group. He recognised three species and three varieties: *E. microtheca* F. Muell. and the variety *cymbaliformis* Blakely and Jacobs, both with persistent dirty, brownish white or dirty grey bark on the bole; *Eucalyptus cyanoclada* Blakely, with rough persistent bark; and *E. coolabah* Blakely and Jacobs, with the varieties *arida* Blakely and *rhodoclada* Blakely. *Eucalyptus coolabah* was said to have persistent rough bark, grey to mealy white on the trunk, smooth and white on secondary branches. A feature of var. *rhodoclada* was reddish branchlets.

Blake (1953) reduced these taxa to two species, *E. microtheca,* including *E. coolabah* and *E. cyanoclada*. Johnston and Marryatt (1965) placed *E. coolabah* and the variety *arida* with *E. microtheca* and considered var. *rhodoclada* of doubtful status. Recently, *E. coolabah* has been reinstated as a distinct species, with var. *arida* as a sub-species (Johnson and Hill 1994). The variety *rhodoclada*, was later named as *E. victrix* (Hill and Johnson 1994). Brooker and Kleinig (1994) provide photographs and distribution maps that suggest unequivocally that *E. victrix* is the correct, current name for the coolibah of the Fortescue Valley.

Distribution of *E. victrix*

According to Brooker and Kleinig (1994), *E. victrix* has a scattered distribution across the Northern Territory and the northern half of Western Australia. It is generally confined to areas such as floodplains and creek sides, often on red clays. Patches of *E. victrix* are found in the south Kimberley, e.g. the Sturt Creek floodplain on cracking clays (lat. 19° 12'S, long. 128° 08'E), (pers. comm. Andrew Mitchell 1998).

In the study area *E. victrix* occurs on red clay soil and tends to occupy the edges or tops of 'gilgai'. Gilgai show pronounced microrelief and are defined as clays possessing marked swelling and shrinking properties; and these soils are vertisols (Isbell 1996). It appears that present populations of *E. victrix* are established on well-flooded sites on the floodplain, mainly along the river channels. The coolibah woodland commences in the vicinity of Ethel Creek Homestead (lat. 22° 54'S, long. 120° 10'E) and then follows the floodplain adjacent to the main channel of the Fortescue River. Coolibah woodland extends north towards the north end of Roy Hill Station near Battle Hill Well (lat. 22°44'S, long. 120° 07'E) (Figure 2).

Description of study area

The study area is located in the upper Fortescue Valley, in the Pilbara district. This lies between the Chichester Plateau to the north and the Hamersley Plateau to the south (Figure 1).

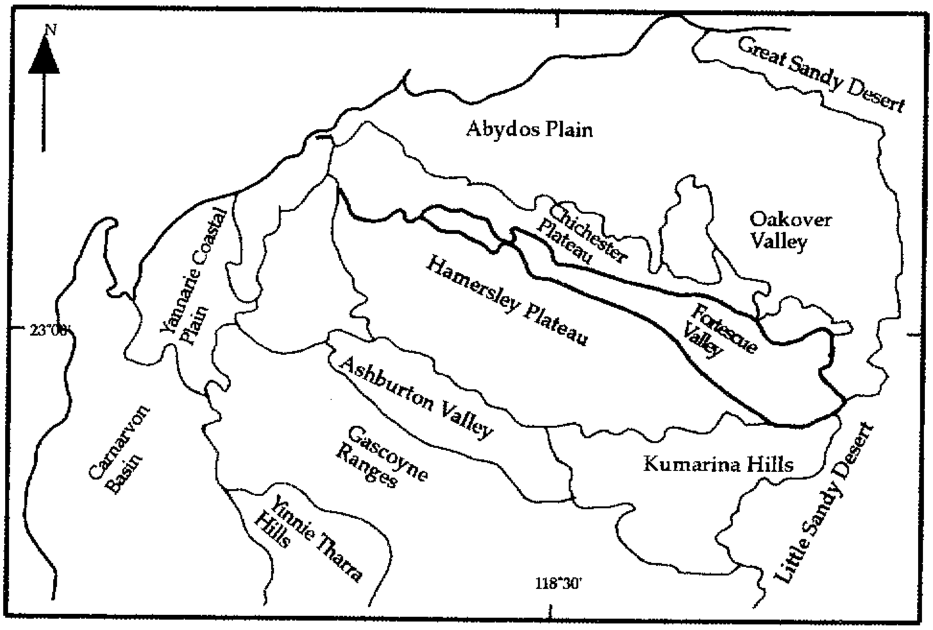


Figure 1: Natural regions and physiographic units of the Pilbara area (after Beard 1975).

Newman (lat. 23° 21'S, long. 119° 44'E), is a mining town in the Pilbara, 544 m above sea level. It was established in early 1968 to accommodate iron-ore mine workers. There are six major pastoral leases near Newman, namely: Bulloo Downs, Ethel Creek, Roy Hill, Marillana, Sylvania and Weelarrana stations. The sites described in this thesis are on Ethel Creek, Roy Hill and Marillana stations, where most of the coolibah woodland is found (Figure 2).

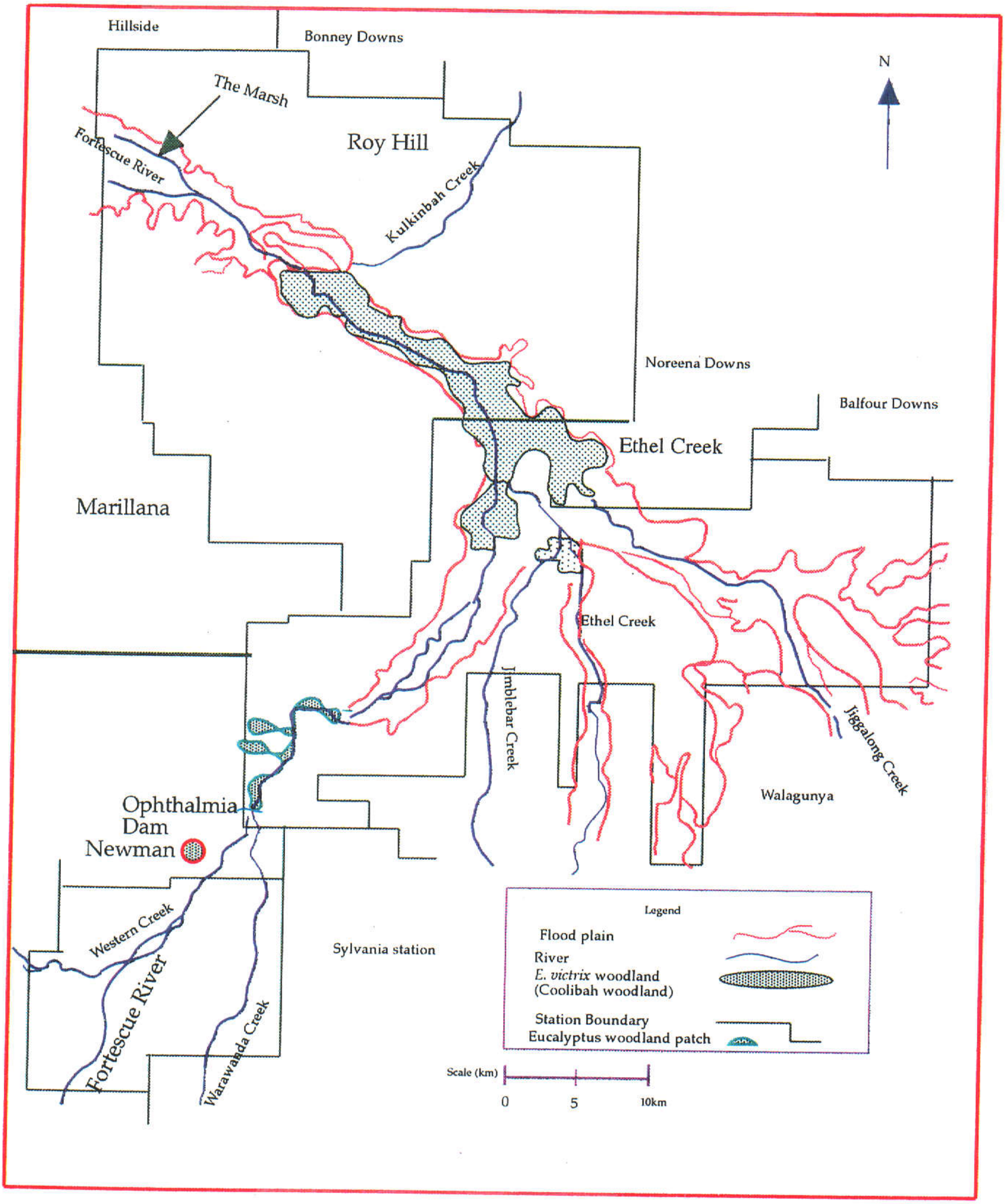


Figure 2: Distribution of coolibah woodland (*E. victrix*) in Fortescue Valley, Pilbara, WA (After Payne and Mitchell 1992).

The Fortescue River has its head waters south of Newman from where it flows north passing through Roy Hill via Ethel Creek and debouches into a large basin, to the north of Roy Hill homestead that extends into Marillana station. This marsh system is located west of Roy Hill Station. It is inundated with flood water after a substantial amount of rainfall (Payne and Mitchell 1992).

The Pilbara climate is arid to semi-arid with mean annual rainfall of 180 to 300 mm. Some 35% of the rain is cyclonic, the remainder mostly received from thunderstorms. Heaviest rainfall usually occurs in the summer months from occasional decaying cyclones that often cause flooding. At Newman, mean maximum and minimum daily temperatures range from 42.1 °C and 27.8 °C in January to 24.0 °C and 8.0 °C in July (Figure 3).

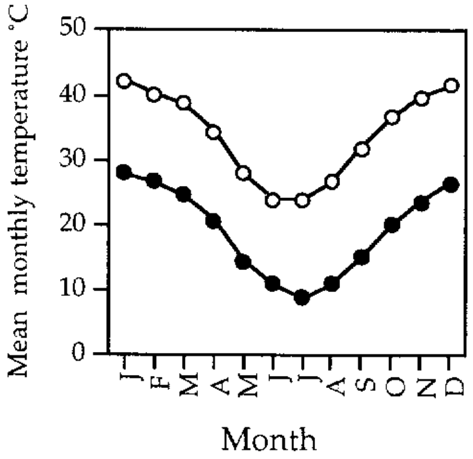


Figure 3: Climatic data at Newman Post Office mean monthly temperatures - open circles maximum; closed circles minimum, (Source: Bureau of Meteorology, 1998).

The Fortescue River was dammed north of Newman in 1981. The Ophthalmia Dam takes its name from the mountain range that runs north of Newman and through which the Fortescue River passes. The dam was constructed to recharge the aquifer feeding the borefield that is used to supply the town of Newman (founded in 1968) and the mine workings associated with digging high grade iron ore from Mt. Whaleback. In the sense that the river now has a dam, it could be described as regulated. However, on the two recent occasions when the upper Fortescue flooded (early 1995 and 1997) the dam quickly overflowed and flood waters extended well up into the floodplain, with a residence time of weeks.

The headwaters of the Fortescue lie in the hills to the south of Newman, particularly on Sylvania station. Heavy rainfall in the catchment results in river flow past Newman and into the dam. The section of river upstream of the dam and for some 50 km downstream, runs through well defined channels with high banks and is filled with gravel beds. In this region the river does not flood out over its banks and there is no present day floodplain. The banks and some parts of the channels carry tall trees of the river red gum (*Eucalyptus camaldulensis* Dehnh.) These are believed to be supplied by aquifers underlying the gravel beds. Some local areas carry stands of *E. victrix,* notably east of the Newman/Marble Bar Rd from the turn off to the Jimblebar Mine and the great bend. In these areas the occurrence of *E. victrix* may be associated with limited flooding of comparatively level, low-lying ground. Near Mary Bore, on Ethel Creek station, the Fortescue divides into an east and a west branch. Further north, near Engine Well, the clearly defined channels further divide into smaller courses that constitute the floodplain proper. Soils are generally loams and show little tendency to aggravated microrelief ('gilgai'). Mixed woodlands of coolibah and *Acacia* species (*e. g. A. citrinoviridis* Tind. & Maslin, *A. distans, A tetragonophylla* Maslin, *A. victoriae* Benth.) in the vicinity of Engine Well have suffered considerable mortality. This was first observed in about 1990 and is believed to be associated with prior overgrazing and a run of comparatively dry years with no extensive flooding (Fox and Wilcox 1992). Since BHP, lessee of Ethel Creek, has reduced cattle stocking levels and undertaken considerable rehabilitation works in degraded areas of the floodplain (non-gilgai soils) from south of Mary Bore to the boundary with Roy Hill station since 1992 (Fox *et al.* 1997a).

From Engine Well, northwards on Ethel Creek station, patches of coolibah woodland occur amongst areas of open grasslands. However, it is not until the vicinity of Jacksons Bore/Walkers Bore that soils become more clayey and are mainly gilgaied. Here, the coolibah woodlands that dominate the landscape on the floodplain are mainly pure stands of *E. victrix*. Other rivers (Jimblebar, Jiggalong) feed into this central part of the Fortescue floodplain, providing opportunities for more severe flooding (when all drainages flood out) or more frequent flood events (as one particular source may flow, when others do not). These coolibah woodlands extend north into Roy Hill station to beyond Battle Hill Well a further 10-12 km to the north west. Near Roy Hill homestead, the beefwood tree (*Grevillea striata* R. Br.) is a common associate of coolibah. At the western extremity of the coolibah woodland, the channels coalesce, debouching into an extensive, shallow marsh ('The Marsh'), some 100 km long and 5-10 km wide. This area has variable amounts of water, but carries few trees along some strand lines. The vegetation is mainly halophytic of low stature samphire (*Halosarcia* spp.) species. The Marsh extends into Marillana station to the west. Other drainage systems originating in the Hamersley Range run north across Marillana ending directly in The Marsh. One such is the Weeli Wolli Creek. The floodplain of this system on Marillana also carries *E. victrix* woodland with some *G. striata* and *Atalaya hemiglauca* (F. Muell.) F. Muell. ex Benth..

Particular sites used in this study are located on each of the three stations, Ethel Creek, Roy Hill and Marillana. Each site is given a locality description, latitude and longitude when first mentioned and is illustrated on a map shown as a figure in the text.

Coolibah woodland and associated vegetation

The vegetation of the coolibah woodland, downstream of Ethel Creek homestead has been formally documented by Beard (1975). The woodland overstorey is dominated by the single species, *E. victrix*. However, mulga (*Acacia aneura* F. Muell. ex Benth.), and *Eucalyptus aspera* F. Muell. trees are found within this woodland. Understorey vegetation is mainly composed of grassy pockets in the woodland.

Grassland

The major grassy patches lie to the south east of the coolibah woodland. The grasslands are characterised by very few scattered *E. victrix* trees. Some 34 grass species, (annual and perennial) have been identified. The most dominant perennial grass species are *Eriachne flaccida* Hartley, *Panicum decompositum* R. Br., and *Chrysopogon fallax* S. T. Blake (Fox 1996). These grass patches are subjected to moderate to heavy grazing pressure by kangaroo and cattle.

Seasonal effects have a dramatic influence on the extent of ground cover. During the summer period, grasses are prominent. If the ground is sufficiently moist from flooding or cyclonic rain, then a number of annual grasses germinate and contribute to ground cover along with perennial grass species. Perhaps the most common and locally abundant annual grass species are *Dactyloctenium radulans* (R. Br.) P. Beauv, *Dichanthium sericeum* (R. Br.) A. Camus, *Chloris pectinata* Benth., *Eragrostis japonica* (Thunb.) Trin. In contrast, during the times when summer rain is lacking (as in 1994 and 1996), annual summer species may not persist and grow very much. Substantial amounts of rainfall later in the year (as in July 1998) will allow further growth of annuals remaining from summer, as well as stimulate winter germination of species of the Asteraceae as in 1998. Good winter rain following poor summer rain tends to favour higher levels of Asteraceae ground cover. In most years the annuals have died off by late September.

In perennial grass communities, the butt-forming grass species e.g. *C. fallax*, *Eragrostis setifolia* Nees, *E. xerophila* Domin, *P. decompositum* are dormant prior to the summer season. With high summer rainfall (November - February) perennial grass species grow new tillers. Shrub species, mainly *Cassia oligophylla* F. Muell. (Caesalpiniaceae), flower during May - July. Trees produce new leaves and initiate flowering during the high rainfall season (Fox *et al.* 1997b).

After a flooding event, flood waters exclude most plant species in lower parts of the woodland. Here species with the ability to withstand inundation can survive whereas other species die back to ground level. Species such as sedges *Cyperus* spp. (Cyperaceae), the fern *Marsilea drummondii* A. Braun or nardoo (Marsileaceae), and of the Scrophulariaceae, *Peplidium muelleri* Benth. and *Peplidium* sp. may seasonally dominate flooded areas.

The following section describes each station's geographical location, rainfall and dominant vegetation.

Ethel Creek Station

Ethel Creek Station (homestead: lat. 22° 54 'S, long. 120° 01'E) (Chapter 2, Figure 5) is used for grazing cattle. The total area is 374, 000 ha. The mean annual rainfall is 264 mm and a large amount of this rainfall is received during the summer months between December - March (Table 1). The rainfall pattern is unpredictable and sporadic.

Within the coolibah woodland there are few other tree species. *E. aspera* is largely confined to the Engine Well area; other, smaller, trees include *A. hemiglauca*, *Hakea suberea* S. Moore., *A. distans* and *G. striata*. The shrub *A. tetragonophylla* is also common. Seasonal ground cover is mainly composed of annual grass species. Some degraded areas have been rehabilitated with the introduced naturalised perennial grasses *Cenchrus ciliaris* L. and *Cenchrus setiger* M. Vahl.. The native perennial grasses *Astrebla pectinata* (Lindley) F. Muell. ex.

Benth., *A. elymoides* Bailey & F. Muell., *E. flaccida* and *E. benthamii* (Domin) Hartley occur in some large stands.

Table 1: Mean, median and maximum monthly rainfall (mm) at Ethel Creek homestead, 1907 - 1994. (excludes 1918, 1922, 1923 & 1982).

Rainfall	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Mean	43.8	57.3	40.8	22.1	24.1	20.5	10.5	5.6	2.3	5.4	7.4	22.8	263.8
Median	31.8	38.2	16.3	4.8	11.4	8.2	1.0	0.0	0.0	0.0	1.3	10.6	236.8
Maximum	309.0	254.2	234.7	211.1	136.4	234.5	103.2	53.4	63.7	63.7	56.7	162.3	814.0

(Source: Bureau of Meteorology, Perth 1998)

Roy Hill Station

Roy Hill Station (homestead: lat. 22° 37'S, long. 119° 57'E) is also used for cattle. It lies north of Ethel Creek station and covers an area of 400, 000 ha. The mean annual rainfall is 261 mm (Table 2).

A few patches of *A. aneura* and *A. victoriae* are found in the woodlands, on Roy Hill. Dominant grass species in this area, include *E. flaccida, E. benthamii* and *P. decompositum. Themeda triandra* Forssk. (kangaroo grass) is also present (Fox and Jeanes 1996).

Table 2: Mean, median and maximum monthly rainfall (mm) at Roy Hill homestead, 1900 - 1990 (excludes 1979).

Rainfall	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Mean	45.0	58.4	44.5	21.9	19.2	18.1	11.2	6.2	1.6	4.9	7.9	23.8	260.9
Median	29.0	39.1	18.8	3.8	8.9	7.4	1.8	0.0	0.0	0.0	2.5	14.4	241.5
Maximum	240.5	333.0	293.7	254.1	129.6	138.9	88.4	98.8	72.2	72.2	58.6	241.0	638.5

(Source: Bureau of Meteorology, Perth 1998)

Marillana Station

Marillana Station (homestead: lat. 22° 38'S, long. 119° 22'E), is to the west of Roy Hill station, occupying 358, 000 ha (appendix 2). Mean annual rainfall is 266 mm (Table 3). An important drainage is the Weeli Wolli Creek.

Trees in the *E. victrix* woodland include *A. hemiglauca* and *G. striata*. The southern part of the coolibah woodland merges into *A. xiphophylla* E. Pritzel, low woodland. Shrub communities are composed of *Acacia tetragonophylla, Acacia synchronicia,* and *C. oligophylla*. Major perennial grass species are *C. fallax, D. sericeum* and *P. decompositum*. Important annual grasses are *E. japonica, Iseilema membranaceum* (Lindley) Domin and *Setaria dielsii* Herrm. in Rosen.

Table 3: Mean, median and maximum monthly rainfall (mm) at Marillana homestead. 1936 - 1997 (excluding 1947, 1984, 1989, 1990, 1992 to 1994).

Rainfall	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Mean	60.2	66.3	43.8	21.2	22.8	20.9	14.3	6.5	1.9	3.8	8.2	20.8	266.4
Median	51.2	43.5	19.3	7.7	10.5	7	3.6	0	0	0	3.1	9.1	234.7
Maximum	269.5	289.3	294.5	124.4	123.6	166.2	174.2	57.2	27.2	27.4	77.2	166.2	774.2

(Source: Bureau of Meteorology, Perth 1998)

Soil of the study area

The Fortescue valley is constituted of quaternary alluvium with some colluvium and sand plains overlying the Tertiary Oakover formation (Beard 1975). Alluvial plains are intermixed with basaltic parent material and are dominated by deep cracking clays. Most soils are earthy clays with some proportions of cracking clays, shallow loams and hard red soils. Flood-out zones have calcareous earths with small areas of shallow calcareous loams, with limestone and kunkar. The study area soils are mainly alluvium- clay, silt and gravel with mixed lacustrine and eolian deposits, mainly composed of silt, clay and sand with some red sands and earthy sands on flanks. At the Marillana site the soil is mainly alluvium with redbrown, clay soil (Thorne and Tyler 1997).

Flooding events

Flooding is a major source of moisture supply to the coolibah woodland (Figure 4). The small channels within the woodland usually feed from the Fortescue after heavy cyclonic rain and thunderstorms (Ng *et al.* 1991). Between 1941 and 1997, a total of 32 cyclonic events were recorded for the Pilbara region (Bureau of Meteorology, Perth 1998) (Appendix 1). It is difficult to correlate the cyclonic events with flooding (pers. comm. Kevin Smith 1998). The thick cloud layer that prevails over the Pilbara region during cyclonic events prevents satellites from supplying clear images of particular areas. However, between 1907 and 1997, Ethel Creek station received more than its average rainfall on 33 occasions. Similarly, Roy Hill (1900 - 1990) 32 times, Marillana (1936 - 1997) 19 times and Newman (1965 - 1997) 17 times (Bureau of Meteorology, Perth 1998).

Figure 4: *E. victrix* woodland during flooding (lat. 22° 49'S, long. 120° 15'E). Photo taken March 1997.

Major rainfall events cause the Fortescue River near Newman to run. At Ethel Creek station the river divides (Figure 2) west of Mary's Bore. Further north at Engine Well the east branch divides into smaller channels. The entire woodland may become flooded after a substantial amount of rain. The present *E. victrix* populations have established along the direction of flow of the river channels and tributaries.

Stock history

The major land use in the area is extensive pastoral grazing with cattle utilising natural vegetation. All three stations carry cattle and a few horses. Payne and Mitchell (1992) reported that Ethel Creek Station carried 9, 000 head of cattle in 1936, numbers were similar in 1960 and 1984. Stock numbers were reduced to 2, 000 during 1997, (pers. comm. Barry Gratte 1997). On Roy Hill Station 14, 000 head were recorded between 1932 and 1936 (Payne and Mitchell 1992) but the numbers were reduced to 3, 000 head in 1992 (Fowler 1993). Overstocking and poor management up to the early 1990's may have contributed significantly to the poor regeneration condition and land degradation recently reported in the Fortescue floodplain (Payne and Mitchell 1992, Fox and Wilcox 1992).

Content of thesis

At the commencement of this study, little was known regarding the Pilbara Coolibah, *E. victrix* and its ecology in the Fortescue River floodplain. This work is an attempt to explain the role of this species in the ecosystem by providing relevant information on factors affecting its life cycle. Several field-based studies are included. In other cases experiments conducted under controlled conditions in the glasshouse or laboratory are reported. Chapter 2 examines the present population structure of several discrete stands of *E. victrix* trees in the woodland. The aims of this chapter are to: explain how size class differences may have arisen; determine whether trees that have flowered and fruited are likely to grow larger; identify the factors affecting height growth of saplings and to determine the conditions that give rise to new seedling recruitment and establishment. The flood tolerance of seedlings of different ages is examined in relation to morphological, physiological and anatomical characteristics in Chapter 3. Chapter 4 provides a comparative study of the flood tolerance of *E. victrix* and two other semi-arid *Eucalyptus* species and Chapter 5 an investigation of the possible association between subordinate species. Chapter 6 examines competition between *E. victrix* and annual and perennial grasses under controlled conditions. In Chapter 7, investigations are reported on the possible allelopathic effects of *E. victrix*, and phenolic compounds produced by *E. victrix* are quantified. Seed longevity is investigated in Chapter 8 and the main findings of this research are synthesised in Chapter 9.

CHAPTER 2

Eucalyptus victrix tree, sapling and seedling populations in the Fortescue River floodplain.

General Introduction

The floodplain of the Fortescue River between the Chichester Plateau in the north and the Hamersley Plateau in the south carries a distinctive, and unique, open woodlands of *E. victrix* among grasslands (Chapter 1). Floodplain communities of *E. victrix* are generally oriented in the direction of river flow. In these grassy woodland, *E. victrix* trees vary somewhat in dimensions. It was speculated that trees of different heights could represent different past recruitment events within fairly large, but well-defined, regions of the floodplain (Fox and O'Connell 1994). This pattern occurs with other floodplain eucalypts (Roberts 1993). However, the extent to which trees of different size occur together in discrete areas of the Fortescue floodplain was not known.

The pattern of seedling recruitment was also not known. Some locations appeared to be able to support seedling *E. victrix* more readily than others. Fox and O'Connell (1994) hypothesised that continuous recruitment may occur in such sites but that transition to larger sizes is dependant on exceptional rainfall / flooding events. It is possible that particular parts of the floodplain may allow the development of trees of larger size than other sites. On the other hand, larger trees on some sites may owe their establishment to an earlier flooding event than in those areas where stands of smaller trees have established. Stands consisting mainly of smaller trees may not be flooded as much as stands consisting mainly of taller trees. Stands of mixed tree size may represent several past recruitment events or differential growth from one establishment event. This could be due either to competition for scarce moisture supplies in periods of no rain and little flooding, or to possible allelopathic effects on seedlings by more mature trees of *E. victrix*.

In general, mortality rates of *Eucalyptus* are very high in the first year of the seedling phase (Stoneman 1992). Species that experience low rainfall regimes have high summer mortality rates (Wellington and Noble 1985a), whilst species that experience high rainfall tend to have higher mortality in winter due to reduced light intensity, frost and fungal attack (Cunningham 1960). Loss of significant numbers of seedlings during summer is attributed to drought and high surface soil temperature (Cunningham 1960, Battaglia and Wilson 1990).

Grazing by native vertebrates can also substantially reduce the seedling population (Gilbert 1961, Leigh and Holgate 1979, Ashton and Chappill 1989). Smaller, younger seedlings are more susceptible to herbivory than are larger older seedlings (Bryant 1971, Leigh and Holgate 1979). Similarly, newly flushed foliage being soft and tender may be more readily digestible by both insects and large herbivores. Older seedlings are more resilient to declining soil moisture than are younger seedlings. Seedlings germinated on a clay soil had a high mortality rate where seedling radicles were on the surface and did not penetrate further in to the soil (Battaglia and Reid 1993). In the floodplain environment, high soil moisture must therefore be a pre-requisite for seed germination and establishment.

Successful germination of most arid-zone plant species can occur only when surface soil retains moisture for five days (Winkworth 1963, Silcock 1973, Burrows 1974). This can only be attained after four days of a reasonable amount of rain (Winkworth 1963). However, the successful establishment of seedlings after germination in the arid-zone is mainly controlled by edaphic factors that affect evaporation, run off and internal drainage (Atkins 1985).

It is believed that rainfall or flooding sufficient to leave standing water for several days, occurs in most summers on at least one occasion over much of the floodplain. Seeds of *E. victrix* fall from the trees and float in standing water. As the wet places dry out, seed deposited on peripheral mud will germinate rapidly. On two recent occasions sufficient rain fell in the headwaters of the Fortescue that the Ophthalmia dam overflowed and much of the woodland remained flooded for several weeks. As a result, large numbers of four to six leaf seedlings were observed in both May 1995 and March 1997 at sites on Marillana and Ethel Creek.

In this Chapter, an examination of present population structure is made of discrete stands of *E. victrix* in the woodlands of the floodplain. The aims are to: explain how size class differences may have originated; determine whether trees that have flowered and fruited are likely to grow larger (in height and bole diameter); identify factors affecting height growth of seedling; and to determine the conditions for new seedling recruitment and establishment. In addition to this, five distinct populations of *E. victrix* are described as numbered population studies.

Population study No. 1. Dimensions of mature *E. victrix* at six discrete floodplain sites

Introduction

To understand the ecology of any particular plant species requires an understanding of present populations and their dynamics *in vivo*. Floodplain species are not exempt from this generalisation. Structure and composition of several floodplain forests in semi-arid and arid parts of Africa have been studied (Hughes 1988). The regeneration and growth of floodplain forest plant species depends on the flooding regime and the balance between dependence on, and tolerance to flooding (Hughes, 1990). Scott *et al.* (1997), demonstrated that 72% of cottonwood (*Populus deltoides*) individuals were established along the Missouri river in a single year when the flow was greater than 1400 m^3/s. Similarly, riparian red gum (*Eucalyptus camaldulensis*) found on the River Murray, requires adequate flooding for growth and recruitment events (Bren 1988). High quality red gum is associated with frequently flooded sites.

In the study area sporadic rain, and variation in flooding events and topography are features of the coolibah woodland. Considerable numbers of *E. victrix* trees grow along the main river channels and in close proximity to minor channels. The main aims of this study were to examine and describe population structure at different sites (Figure 5) and also to document any variation in tree dimensions between sites.

Hypothesis

It was hypothesised that no differences in height and stem diameter of *E. victrix* trees found in different sites.

Methods

Six populations of *E. victrix* were selected for measurement and enumerated between 5 May and 27 September 1995 (Table 4). The aim was to measure approximately 100 trees at each site. The mid-lines of five transects were marked with star pickets. The single rectangular plot was marked with iron pickets at the four corners. All trees were tagged with numbered metal tags and. The heights of tall trees were measured using a Clinometer (Suunto Co., Helsinki, Finland) for tall trees. Trees less than 8 m were measured with extendable carpenter's tape. Tree heights were obtained on three separate occasions (Table 4). Stem diameters were taken only in 1997, with a diameter tape at 1.3 m (dbh). Trees were grouped by height into 13, 1 m intervals, and by stem diameter into 13 groups of 4 cm intervals. Using the following relative growth rate formula (RGR) $RGR = \frac{\log eh_2 - \log eh_1}{t_2 - t_1}$ mean height growth rate was calculated.

Table 4: Transect details: Ethel Creek, Roy Hill and Marillana stations.

Site	Location	Station	Length (m) (area m^2)	n =	Dates of measurement		
1	lat. 22° 50'S, long. 120° 12'E	Ethel Creek	112 (5,600)	100	27. 9. 95	23. 2. 96	15. 3. 97
2	lat. 22° 50'S, long. 120° 12'E	Ethel Creek	171 (8,550)	100	25. 9. 95	16. 2.96	16. 3. 97
3	lat. 22° 45'S, long. 120° 08'E	Roy Hill	188 (3,760)	102	05. 5. 95	14. 2.96	10.3.97
4	lat. 22° 46'S, long. 120° 09'E	Roy Hill	80 (4,000)	101	06. 7. 95	23. 2.96	18. 3. 97
5*	lat. 22° 48'S, long. 120° 11'E	Roy Hill	80 (1,600)	100	07. 7. 95	22. 2. 96	20. 3. 97
6	lat. 22° 29'S, long. 119° 14'E	Marillana	133 (6,650)	125	18. 9. 95	19. 2. 96	23. 3. 97

* site 5 was a rectangular plot of 50 x 80 m.

Statistical analyses

Data were analysed using the Super ANOVA software program (Abacus Concepts, Berkley, California) by one-way analysis of variance of height and stem diameters. Residual plots of each ANOVA were obtained to examine homogeneity of variance. All stem diameters were quadratic means derived using $r = \sqrt{\sum \pi r^2/\pi}$, where $\sum \pi$ represents more than 1 stem per tree. Means were compared using Tukey's HSD comparison (Day and Quinn 1989).

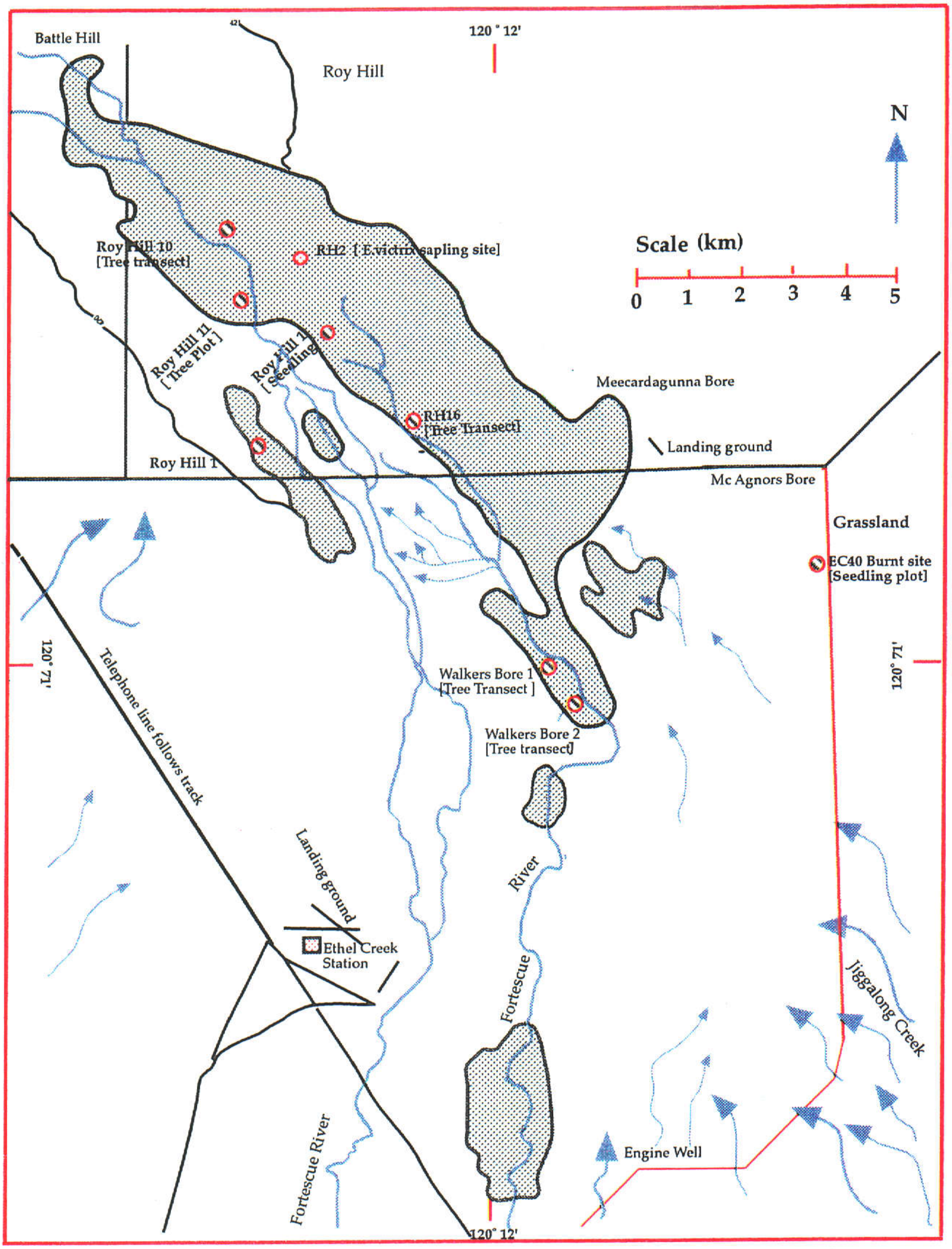


Figure 5: Location of sampling sites of *E. victrix* trees, Ethel Creek - (site 1) Walkers Bore 1, (site 2) Walkers Bore 2; Roy Hill - (site 3) RH 10, (site 4) RH 11 & (site 5) RH16, Saplings RH 2. Seedlings at Ethel Creek burnt grassland: EC40. Black lines are tracks, green lines are boundary between Roy Hill (North) and Ethel Creek (South) stations, closed green patches represent coolibah woodland. Small blue wriggle lines are direction of water flow.

Results

To describe the present population structure of *E. victrix,* tree height data for 1997 were used. A total of 628 trees was measured at the six sites. Height class distribution of *E. victrix* trees measured at the six sites shows peaks vary between sites. The tallest trees measured were 12.20 and 12.92 m at sites 1 and 2 respectively. No plants of less than 1 m tall were present at this sites. At sites 3 and 5 trees did not exceed 6 m in height.

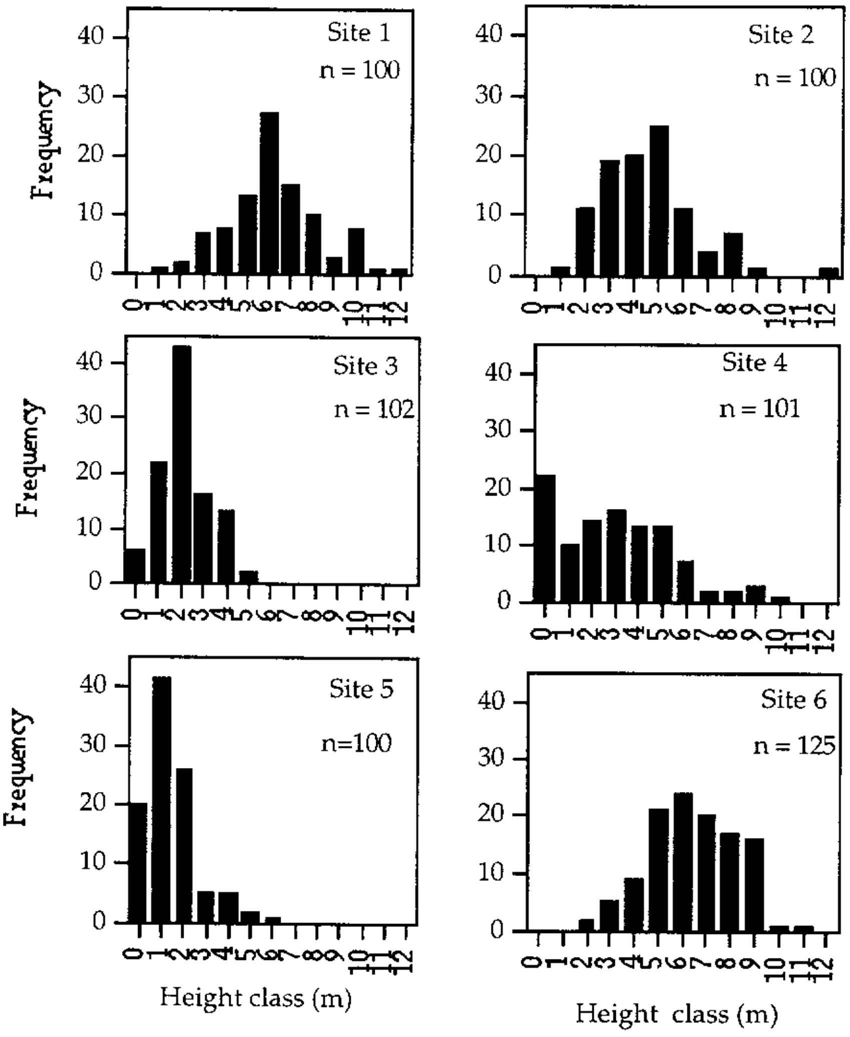


Figure 6: Trees arranged by height class for six sets of *E. victrix* trees 10 - 23 March 1997. (Sites as in Table 4).

The presence of individuals less than 1 m tall suggests that continuous recruitment may have been occurring at sites 3, 4, and 5. Sixty percent (n = 60) of the trees are between 5 - 8 m height in site 1, similar to site 6, with 52% (n =

65) in this range. Of the total (628 trees) 15% (n = 98), and 13% (n = 83) are less than 3 and 6 m tall respectively (Figure 6).

Mean heights of *E. victrix*, varied significantly (P = 0.001***) between sites. The tallest mean height was initially found at site 1, but site 6 appeared to have tallest trees at subsequent measurements. Shortest mean height was found consistently at site 5, where mean tree height did not exceed 1.96 m (Table 5).

Table 5: Mean height (± SD) of measured *E. victrix* trees 1995 - 1997.

Transect	n =	1995 Mean (± SD)	1996 Mean (± SD)	1997 Mean (± SD)
Site 1	100	6.86 (2.07)^{a}	6.91 (2.17)^{a}	6.68 (2.07)^{a}
Site 2	100	5.77 (2.07)^{b}	5.50 (2.18)^{b}	5.05 (1.88)^{b}
Site 3	102	2.40 (1.16)^{c}	2.41 (1.18)^{d}	2.64 (1.12)^{c}
Site 4	101	3.87 (2.03)^{b}	3.77(2.43)^{c}	3.62 (2.45)^{c}
Site 5	100	1.96 (0.19)^{d}	1.87 (1.16)^{d}	1.95 (1.16)^{d}
Site 6	125	6.50 (1.86)^{ab}	7.13 (1.55)^{a}	7.14 (1.99)^{a}
P =		***	***	***

Significant differences between measurements at sites are indicated by ***P <0.001. Different letters indicate means are significantly different between sites using Tukey's HSD comparison. Dates as in Table 4.

Stem diameter class data are shown in Figure 7. The biggest stem diameter (51.54 cm) was measured at site 6. At site 3, trees did not exceed 12 cm in diameter. At that site, 51% (n = 36, total number of trees measured = 70) of trees were found in the 4 - 8 cm diameter class. In contrast, at site 6, distribution by diameter class shows a normal distribution and a considerable number of trees (23%, n = 29, total number of trees measured = 125) were found in the 20-24 cm diameter class.

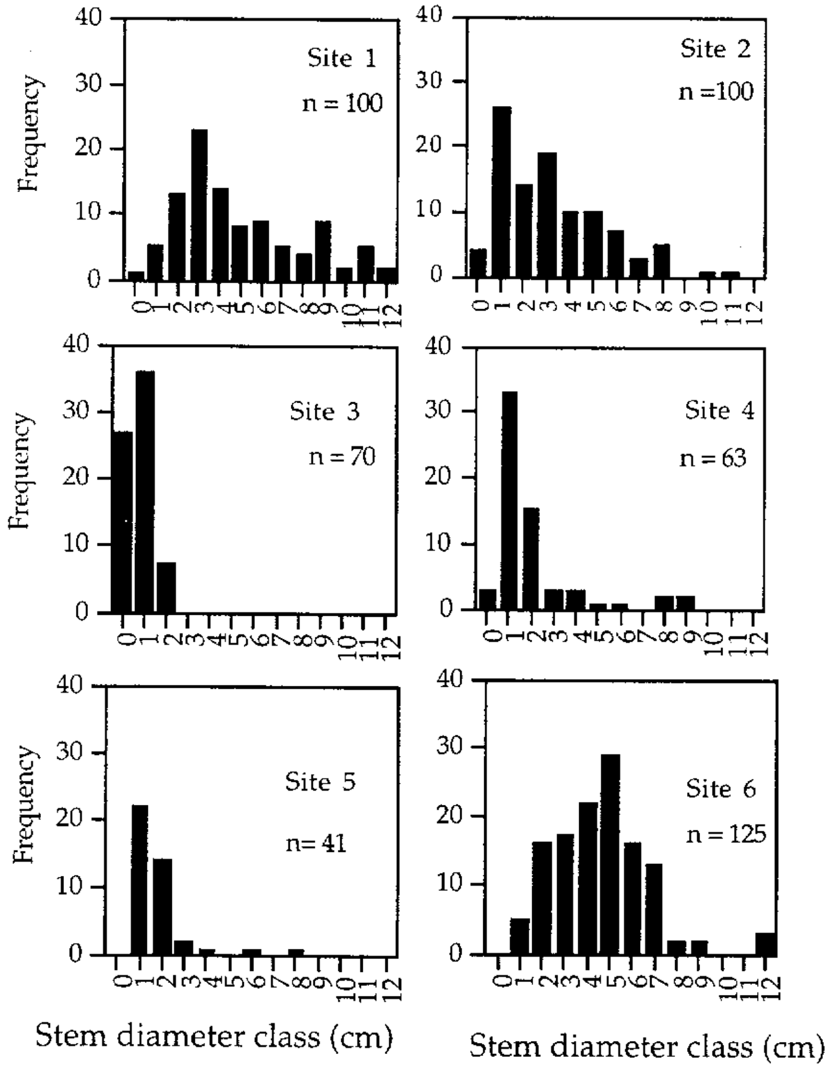


Figure 7: Stem diameter frequency class for six sets of *E. victrix* trees 10 - 23 March 1997. (Sites as in Table 4).

Sub-sets of (n = 25) the tallest trees were selected from each site. Analysis of variance revealed that mean height varied significantly (P= 0.001***) between sites (Table 6). Heights of taller trees were probably overestimated at sites 2, 4 and 5 at the first measurement.

Similarly, sub-sets of smaller trees were selected for analysis of variance. Significant differences were observed between sites (Table 7). Sites 1 and 6 had tallest plants in the smallest tree sub- sets. Heights were generally lower at the second measurement (1996) except in site 6. By the third measurement (1997) trees appear to have increased in height, except for sites 4 and 6. Shorter trees at site 2 were probably overestimated at the first measurement.

Table 6: Sub-set of mean height (± SD) m of tallest trees measured at different sites 1995 - 1997.

Transect	n =	1995	1996	1997
		Mean (± SD)	Mean (± SD)	Mean (± SD)
Site 1	25	9.37 (1.14)^{a}	9.54 (1.14)^{a}	9.43 (1.16)^{a}
Site 2	25	8.33 (1.23)^{a}	8.23 (1.47)^{b}	7.53 (1.60)^{b}
Site 3	25	3.98 (0.61)^{b}	3.99 (0.73)^{d}	4.16 (0.62)^{c}
Site 4	25	7.99 (6.00)^{a}	7.11 (1.02)^{c}	6.89 (1.67)^{b}
Site 5	25	4.09 (2.95)^{b}	3.46 (1.09)^{d}	3.55 (1.04)^{c}
Site 6	25	8.98 (0.68)^{a}	9.22 (0.62)^{a}	9.98 (0.76)^{a}
P =		***	***	***

Significant differences between measurements at sites are indicated by ***P <0.001. Different letters indicate means are significantly different between sites using Tukey's HSD comparison.

Table 7: Sub-set of mean height (± SD) m of smaller trees measured at different sites 1995 - 1997.

Transect	n =	1995	1996	1997
		Mean (± SD)	Mean (± SD)	Mean (± SD)
Site 1	25	4.11 (1.07)^{a}	3.97 (0.99)^{b}	4.21 (1.08)^{a}
Site 2	25	3.05 (0.64)^{b}	2.81 (0.58)^{c}	2.95 (0.56)^{b}
Site 3	25	0.96 (0.27)^{c}	0.95 (0.32)^{d}	1.25 (0.44)^{d}
Site 4	25	0.73 (0.35)^{c}	0.76 (0.37)^{d}	0.71 (0.32)^{d}
Site 5	25	0.71 (0.15)^{c}	0.77 (0.14)^{d}	0.84 (0.16)^{d}
Site 6	25	3.73 (1.00)^{a}	4.87 (0.74)a	4.45 (0.75)^{a}
P =		***	***	***

Significant differences between measurements at sites are indicated by ***P <0.001. Different letters indicate means are significantly different between sites using Tukey's HSD comparison.

Mean stem diameter varied significantly (P = 0.001***) between sites. Largest and smallest sub-sets of stem diameter data also show significant differences except that sites 1 and 6 were not significantly different. Largest stem diameters for sub-sets also came from sites 1 and 6 (Table 8).

Table 8: Mean stem diameter (cm) of measured *E. victrix* trees 1997. Sub-set of mean stem diameter (cm) of smallest and largest diameters measured at different sites 1997.

Transect	n =	All data	n =	Largest sub-set	n =	Smallest sub-set
		Mean (± SD)		Mean (± SD)		Mean (± SD)
Site 1	100	21.62 (11.88)^{a}	25	39.02 (5.83)^{a}	25	9.71 (2.69)^{a}
Site 2	100	14.45 (9.52)^{b}	25	27.71 (7.64)^{b}	25	5.23 (1.31)^{b}
Site 3	70	4.98 (1.96)^{d}	25	7.17 (1.22)^{d}	25	3.06 (0.71)^{c}
Site 4	63	10.26 (8.44)^{c}	25	16.94 (10.18)^{c}	25	5.06 (1.17)^{b}
Site 5	41	6.38 (5.45)^{d}	15	10.32 (7.57)^{d}	25	4.07 (0.83)^{ab}
Site 6	125	20.47(8.55)^{a}	25	32.69 (7.46)^{a}	25	9.66 (2.14)^{a}
P =		***		***		***

Significant differences between measurements at sites are indicated by ****P* <0.001. Different letters indicate means are significantly different between sites using Tukey's HSD comparison. Except site 5, largest sub-set diameter n =15, all the other sites n = 25.

Relative growth rate in height (RGR) was calculated for trees measured at each of the 6 sites. The graphs presented in figure 8 suggest that only slight variations were observed in height. In the period to the first measurement, the Ophthalmia Dam had overflowed and Ethel Creek had received 350 mm of rain fall between January and July 1995. Trees may have used this favourable state of abundant moisture and produced new leaves prior to the first measurement (September 1995). By the third measurement (1997) marginal reductions were observed in mean height of trees measured at sites 1, 2, 4 and 6. In contrast, sites 3 and 5 had a slight increase in height (Figure 8).

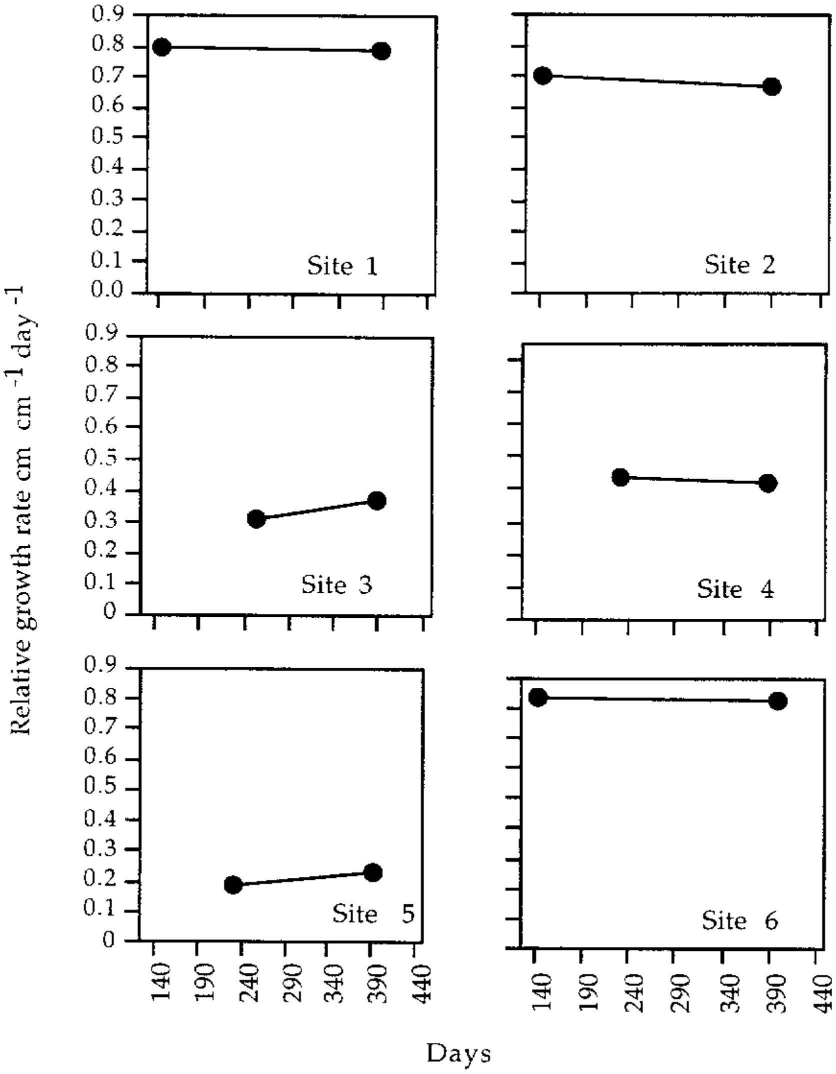


Figure 8: Relative growth rate (cm cm $^{-1}$ day^{-1}) of *E. victrix* trees measured at six discrete sites in Fortescue floodplain between March 1995 - March 1997.

Population study No. 2. Dimensions and survival of a sapling cohort of *E. victrix* at Roy Hill station (1995 - 97)

Introduction

Knowledge of the long term population demography of woody species in arid and semi arid regions is limited (Grice *et al.* 1994). Although no data on demography of seedlings, saplings or trees have been published for *E. victrix*, information on other members of this genus has provided some base-line information for this study. *Eucalyptus coolabah* subsp. *arida* regeneration is one model that probably applies to that of other riparian species. Roberts (1993), found that recently recruited *Eucalyptus coolabah* subsp. *arida* was confined to an unique topographic position: top of a steep river bank and on a sand mound. Similarly Russell *et al.* (1967) examined *A. harpophylla* (brigalow) growth, microrelief and chemical properties in relation to gilgai soil. They found that mature trees of *A. harpophylla* tend to be confined to the higher segments of microrelief. Trees confined on the higher part of the gilgai grow taller.

A population of *E. victrix* saplings (initially less than 2 m tall) was studied from 1995 to 1997.

Hypothesis

The growth of *E. victrix* saplings is not affected by the micro-topography.

Methods

In 1995 a considerable number of *E. victrix* saplings less than 2 m in height was observed growing in Roy Hill in the vicinity of plot RH2, (lat. 22° 46'S, long. 120° 10'E). One hundred saplings were selected in April 1995, tagged with numbered metal tags and their heights measured (cm). These saplings were again measured in September 1995. During July 1996, sapling habitat was classified as one of: in the gilgai, edge of the gilgai or top of the gilgai (Figure 9). In September 1997, stem diameters were measured with a digital calliper at

10 cm from the ground. These measurements were used to calculate stem diameter $r = \sqrt{\sum \pi r^2 / \pi}$. In both 1996 and 1997 saplings were remeasured four times; February, May, June and October of 1996; and in February, May, July and September of 1997.

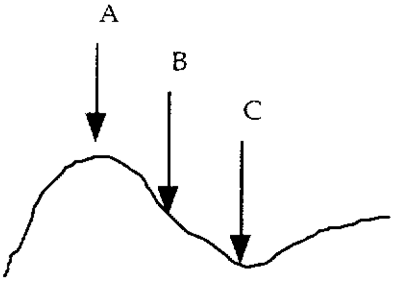


Figure 9: Diagrammatic representation showing position of gilgai. Top of the gilgai (A); edge of the gilgai (B) and inside the gilgai (C).

In September 1997, stem taper was obtained. A sub-set of single, straight-stemmed individuals (n = 15) was selected from the set of 100 tagged saplings. Diameters were measured at 10 cm intervals from 10 cm above the soil surface. Mean height growth rate was calculated using the following relative growth rate formula (RGR) $RGR = \frac{\log eh_2 - \log eh_1}{t_2 - t_1}$.

Height classes of 20 cm were used to examine frequency distribution from 0 to less than 20 cm (class 1) to 280 to 300 cm (class 15). Similarly, for bole diameter, 10 mm classes were used from 0 to less than 10 mm (class 1) to 70 to less than 80 mm (class 8).

Results

No mortality was recorded during the study period. The September 1995 height class distribution is a typical normal distribution and confirms this cohort (94.94 ± SD 32.27 cm) reflects a single recruitment event. In contrast, by September 1997, two years later, the population reveals two different peaks in height class. Most saplings fell in the 80 - 100 cm height class during 1995, whereas most (n = 16) are in the 200 - 219.9 cm class at 1997 (Figure 10).

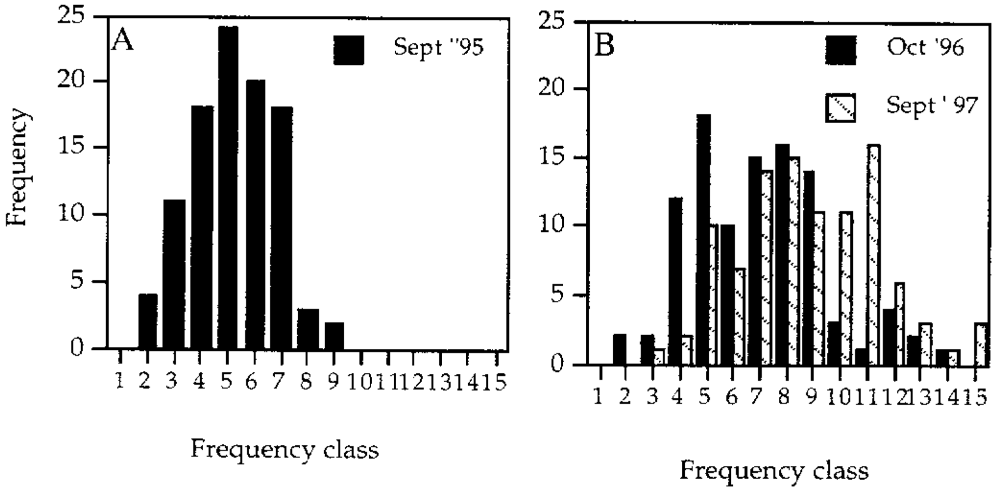


Figure 10 A: September 1995 height - frequency class distribution of *E. victrix*. **B:** October 1996 & September 1997 height - frequency class distributions of *E. victrix* (n =100 throughout).

The stem diameter class distribution of saplings at September 1997 showed a predominance of individuals in the 50 less than 59.99 (mm) class (29%) and only 1% in the largest size class (70 to 80 mm) (Figure 11).

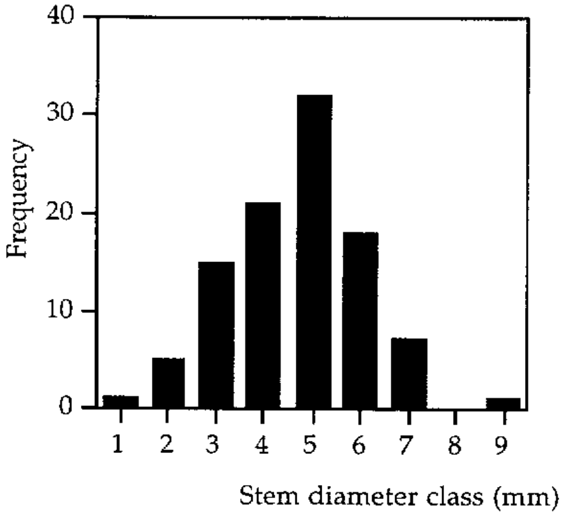


Figure 11: Stem diameter frequency class distribution September 1997 (n = 100). Diameter classes are 10 mm, class 1 = less than 10 mm; class 9 = 80 to 90 mm.

Mean heights of all tagged saplings over the period 1995 - 1997 showed a gradual increase from 90 to 160 cm (Figure 12).

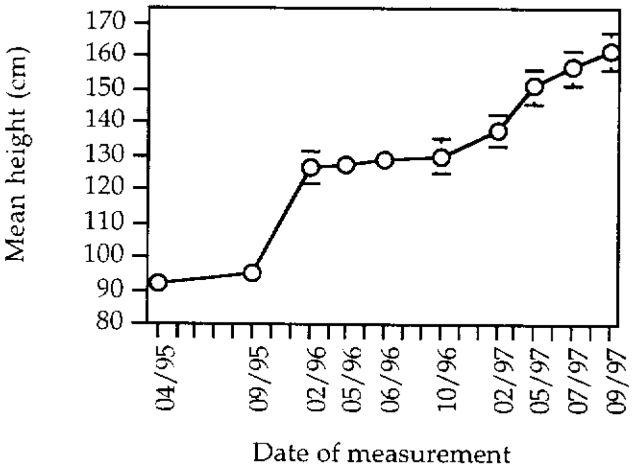


Figure 12: Mean height of RH2 *E. victrix* saplings over a period of 29 months. Bars indicate standard deviations (n = 100).

A correlation between height (m) and stem diameter (mm) was observed at September 1997 (Figure 13). This is significant: Sapling height (m) = 0.032 stem diameter (mm) + 0.347, (n = 100, r^2 = 0.660, $P = 0.001^{***}$)

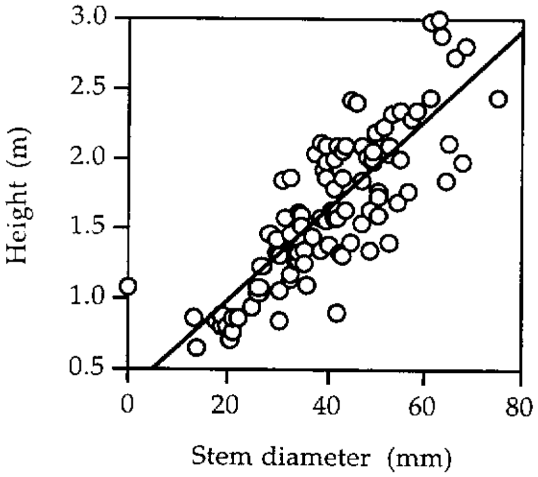


Figure 13: Sapling height and stem diameter of *E. victrix*, in September 1997.

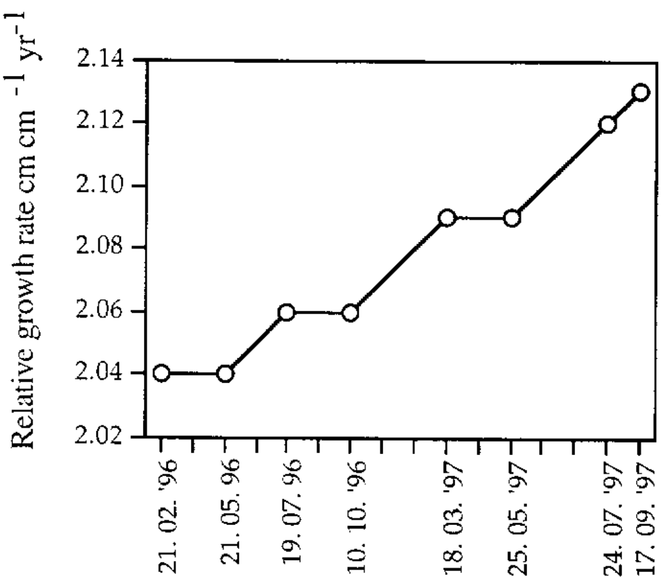


Figure 14: Relative growth rate in height of *E. victrix* saplings.

The relative growth rate curve between September 1995 and September 1997 is shown in Figure 14. The overall trend is positive growth, although a slight decline was observed between February and May 1996 measurements.

The most common feature in *E. victrix* trees is of a single dominant stem, but in saplings up to 5 additional stems arise from a lignotuber. Single stemmed sapling measurements show that stem taper is uniform (Figure 15).

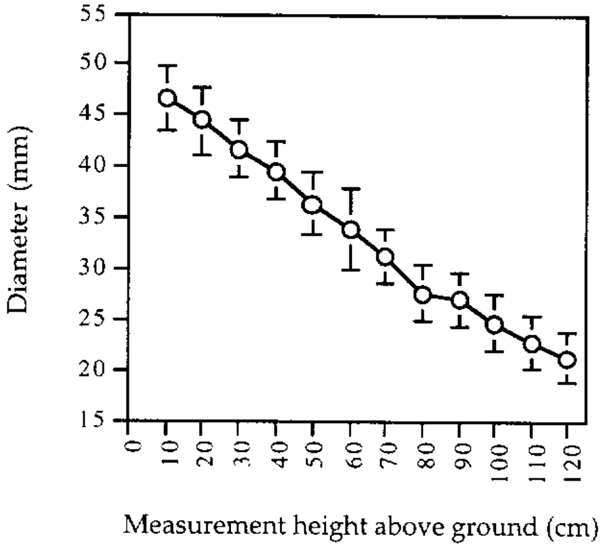


Figure 15: Mean stem diameters (mm) for 15 single stemmed saplings measured at 10 cm intervals from the base, September 1997. Vertical bars are standard errors.

In September 1995, many saplings had more than one stem growing from the base. Mean heights were not significantly different for plants with different numbers of stems (Table 9). Of the 100 saplings, 85% were branched between 10 - 15 cm from the lignotuber and 16% had 6 or more branches.

Table 9: Mean height m (± SD) of *E. victrix* saplings by number of stems.

No of stems	n = 100	Sept. 1995	Oct. 1996	Sept. 1997
1	15	1.04 (± 0.36)	1.28 (± 0.52)	1.63 (± 0.60)
2	23	1.00 (± 0.30)	1.27 (± 0.46)	1.63 (± 0.45)
3	20	1.02 (± 0.23)	1.43 (± 0.52)	1.83 (± 0.57)
4	9	0.78 (± 0.19)	0.96 (± 0.41)	1.35 (± 0.46)
5	17	0.89 (± 0.33)	1.40 (± 0.43)	1.74 (± 0.49)
6 +	16	0.88 (± 0.36)	1.20 (± 0.55)	1.57 (± 0.60)
F =		1.44	1.48	1.18
P =		NS	NS	NS

NS = Not significant.

Microsite variation and height of *E. victrix* saplings

Saplings on the edge of gilgai grew taller than those in the gilgai. Those in the gilgai generally had significantly lower height (Table 10).

The whole area (RH2) is typical gilgai with mounds and depressions. Of the 100 saplings, 35% were found in the gilgai, 38% on the edge of the gilgai with the remaining 27% on top of the gilgai (Table 10).

Mean height by microsite position varied, with slight falls observed for those on the top of the gilgai at the fourth measurement (May 1996). By February 1997 mean height was the same as that measured in February 1996 and it increased gradually up to September 1997 (Table 10).

Table 10: Mean height cm (± SD) of *E. victrix* saplings by microsite.

Date of measurement	In (n = 35)	Top (n = 27)	Edge (n = 38)	F =	*P* =
1995 Apr.	0.84 ± 0.29^{b}	0.89 ± 0.28^{ab}	1.02 ± 0.28^{a}	4.13	*
1995 Sep.	0.80 ± 0.27^{b}	0.96 ± 0.29^{a}	1.09 ± 0.29^{a}	9.17	***
1996 Feb.	1.06 ± 0.42^{b}	1.36 ± 0.61^{a}	1.39 ± 0.46^{a}	4.68	**
1996 May	1.07 ± 0.33^{b}	1.25 ± 0.48^{ab}	1.41 ± 0.47^{a}	5.99	**
1996 Jul.	1.08 ± 0.34^{b}	1.26 ± 0.40^{ab}	1.47 ± 0.49^{a}	7.71	***
1996 Oct.	1.08 ± 0.35^{b}	1.20 ± 0.44^{b}	1.54 ± 0.54^{a}	9.60	***
1997 Feb.	1.15 ± 0.38^{b}	1.36 ± 0.45^{ab}	1.59 ± 0.55^{a}	8.03	***
1997 May	1.28 ± 0.42^{b}	1.41 ± 0.48^{b}	1.71 ± 0.51^{a}	8.25	***
1997 Jul.	1.38 ± 0.39^{b}	1.57 ± 0.41^{b}	1.87 ± 0.55^{a}	9.98	***
1997 Sep.	1.40 ± 0.42^{b}	1.61 ± 0.48^{b}	1.92 ± 0.55^{a}	10.30	***

Significant differences are *$P < 0.05$; **$P < 0.01$, ***$P < 0.001$. Different letters indicate means are significantly different (Tukey's HSD test).

Mean stem diameter is significantly lower for saplings in the gilgai than on the top or the edge of the gilgai (Table 11)

Table 11: Analysis of variance table for the microsite variation effect of mean stem diameter (mm) of *E. victrix* saplings measured in September 1997.

Date of measurement	In (n = 35) Mean ± SD	Top (n = 27) Mean ± SD	Edge (n = 38) Mean ± SD	F value	*P* value
1997 Sep	34.92^{b} ± 2.02	41.09^{a} ± 2.34	46.47^{a} ± 12.85	7.95	***

Significant differences between measurements at sites are indicated by ***P <0.001. Different letters indicate means are significantly different (Tukey's HSD test).

Population study No. 3 Pilot study of *E. victrix* seedling demography

Introduction

In this section an account is given of a pilot study to examine the fate of a cohort of small seedlings of *E. victrix*. In early 1995, extensive flooding on Ethel Creek and Roy Hill in the coolibah woodlands was accompanied by similar conditions at the Marillana site in the Weeli Wolli floodplain. Marillana homestead (lat. 22° 38'S, long. 119° 24'E) had 392 mm of rainfall in January and February 1995. The Marillana site could not be visited in February due to flooded conditions. When the area was visited on May 3, a number of recently established *E. victrix* seedlings was found inside the exclosure (lat. 22° 29'S, long. 119° 14'E). This provided an opportunity to examine the fate of new seedlings in an area where none had been noted over the previous three years. It was assumed that they had originated in the period following flood water recession, between late February and March 1995.

Hypothesis

As the seedlings were in close proximity to mature trees, it was hypothesised that they would not persist due to root competition.

Methods

Fifty two seedlings of *E. victrix* were found in an area of 160 m^2 (20 x 8 m), inside a standard 20 x 25 m plot. Their height was measured in cm to the nearest mm and they were scored for number of leaves present. Each plant was mapped and tagged with plastic flagging attached to a short fence-wire stake, and the distance to the nearest *E. victrix* tree was recorded. Seedlings were measured opportunistically over the following 250 days until they had all died (18. 02. 1996). Within the 500 m^2 plot, eight mature trees of *E. victrix* were present, ranging in height from 6 to 10 m.

Results

At first measurement the 52 seedlings ranged in height from 1 to 10 cm and had between 5 and 10 leaves. They were between 0.5 and 5 m from the nearest *E. victrix* tree. Seedlings were concentrated in two patches: one of 7 x 4 m held 33 seedlings; the other of 10 x 3 m held 17 seedlings. These represent local densities of 1.18 and 0.57 plants per m^2 respectively.

In May 1995, the modal height class was 4 cm (Figure 16). Mean height was 4.78 (SD ± 2.07) cm with a mean of 7.78 (SD ± 1.43) leaves. A few individuals (2%) were in the largest height class of 10.1 - 11 cm.

By June 1995, 46% of seedlings were observed to have been damaged by insects. The mean height was 5.30 (SD ± 4.21) cm (n= 45) with mean leaf number 6.23 (SD ± 3.94). By September 1995, the mean height was 7.69 (SD ± 3.74) cm (n= 28) with a mean of 6.54 (SD ± 2.85) leaves.

Subsequently 13% (n = 7) and 65% (n= 34) of seedlings died by June and September 1995 respectively.

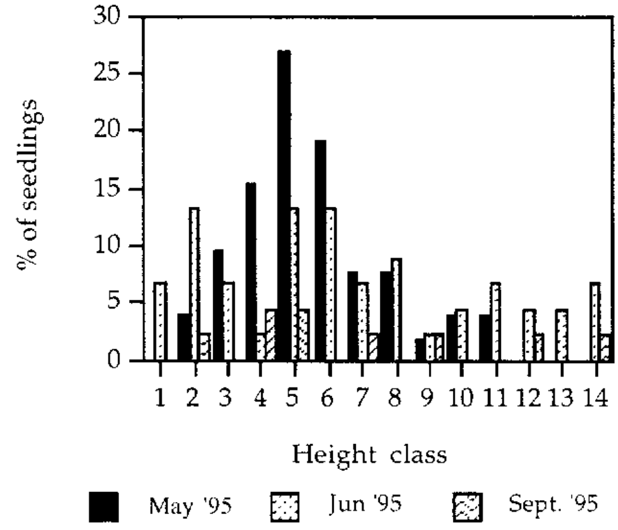


Figure 16: Size class distribution of *E. victrix* seedlings in May, June and Sept. 1995 at Marillana exclosure, by 1 cm intervals.

By September 1995, mean seedling height was further reduced and a considerable number of seedlings were dead. All seedlings had died by February 1996.

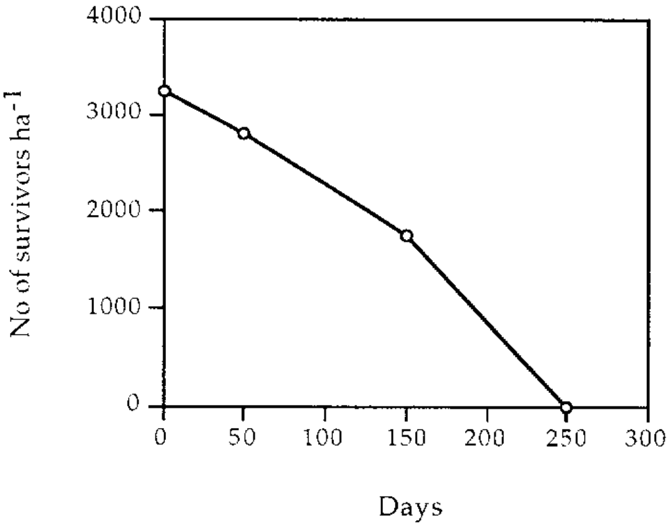


Figure 17: Survivorship curve for *E. victrix* seedlings in pilot study at Marillana exclosure (0 = 03. 05. 1995, 250 = 26. 09. 1995).

Seedling density was 3250 seedlings ha^{-1} at May 1995, falling to 2812 ha^{-1} by 23 June 1995. By 26 September 1995, density had fallen to 1750 ha^{-1} (Figure 17).

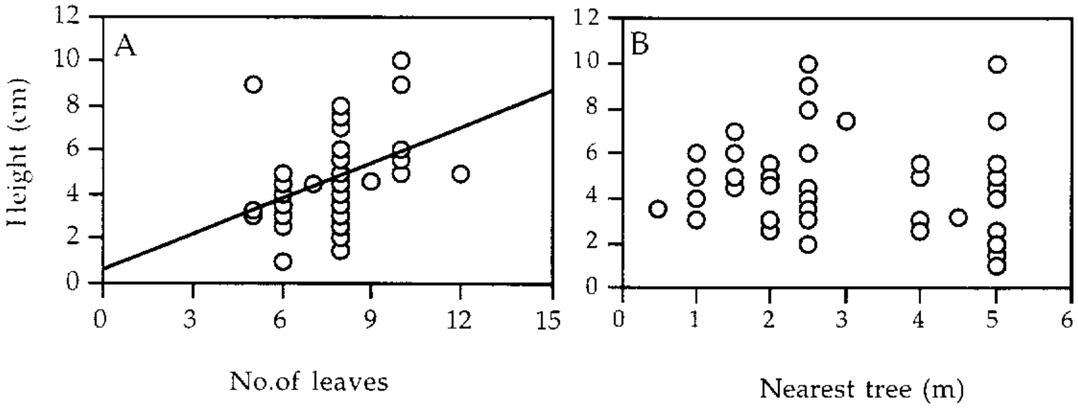


Figure 18: Seedling heights regressed against A: number of leaves and B: nearest tree at 03. 05. 1995, in pilot study at Marillana.

Regression of seedling height on number of leaves at 3 May 1995 shows a linear relationship (Figure 18A), the regression is height (cm) = 0.387 + 0.57 number of leaves ($r^2 = 0.155$, $P = 0.0038$**, n = 52). In contrast, seedling heights (cm) were independent of distance to nearest *E. victrix* tree. The regression is seedling height (cm) = 5.272 - 0.158 nearest tree (m) ($r^2 = 0.012$, $P = 0.4391^{NS}$, n = 52) (Figure 18B).

Relative growth rate of seedlings was calculated from the first measurement (3 May 1995). Relative growth rate declined over the 4 month period, coincident with much leaf loss due to herbivory (Figure 19).

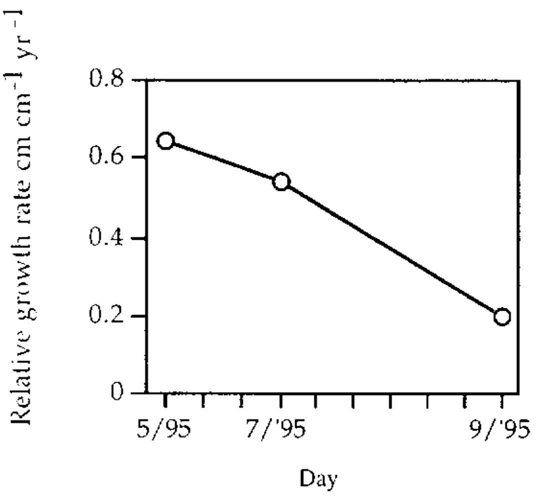


Figure 19: Relative growth rate (height) for *E. victrix* seedlings in pilot study at Marillana exclosure.

Population study No. 4. Seedling monitoring 1997 - 1998

Introduction

Following the pilot seedling study of 1995, efforts were made to locate fresh seedlings during subsequent visits to sites in the Fortescue Floodplain on Ethel Creek and Roy Hill stations, as well as on the Marillana site in the Weeli Wolli floodplain. Rainfall of 275 mm at Ethel Creek and 160 mm at Marillana homestead were recorded for 1996. These were less than in 1995, no over-bank flooding of the Fortescue River was observed and no *E. victrix* were found. In 1997, over-bank flooding occurred in the Fortescue floodplain and new seedlings were observed at the Marillana sites. These seedlings were measured until February 1998.

Hypothesis

the survival of seedlings is not dependent on subsequent rainfall.

Methods

Two hundred and sixty nine seedlings of *E. victrix* were found and tagged as before in a total area of 260 m^2 at Marillana during March 1997. Sets of 32, 58, 73, and 106 *E. victrix* seedlings were recorded in areas of 30, 200, 24 and 6 m^2 respectively. Seedlings were measured on 23 March and 21 September 1997. The measurements and seedling markings were as for the pilot study. For the first 26 seedlings, stem diameter was obtained using digital callipers just above the soil surface .

Results

Most seedlings (39%, n= 105) were 1-2 cm tall. The peak reflected a single recent recruitment event (Figure 20). Mean seedling height on 23 March 1997 was 0. 74 (SD ± 0.39) cm, with a mean of 2.33 (SD ± 1.42) leaves (n = 269). By 21 of September 1997 mean height was 6.36 (SD ± 2.91) cm, and the mean number of leaves was 9.65 (SD ± 2.65) (n = 95).

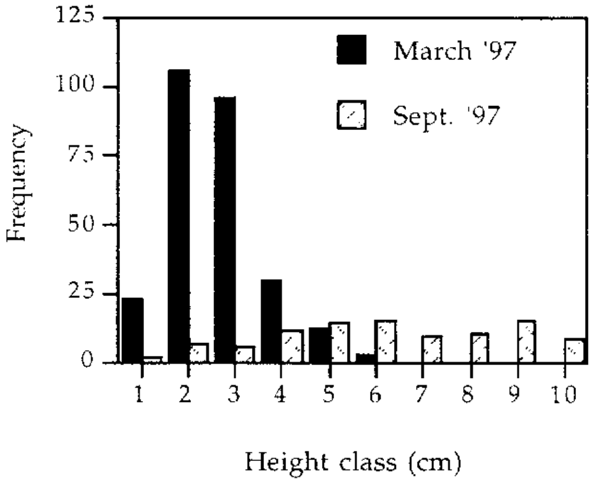


Figure 20: Size class distribution of *E. victrix* seedlings measured at Marillana sites during 1997.

The regression equation between seedling height (cm) and stem diameter (mm) gave a positive and significant correlation, the regression is: stem height (cm) = 1.361 + 0.601 (stem diameter) (mm), (n = 26, r^2 = 0.18, P = 0.0313*) (Figure 21).

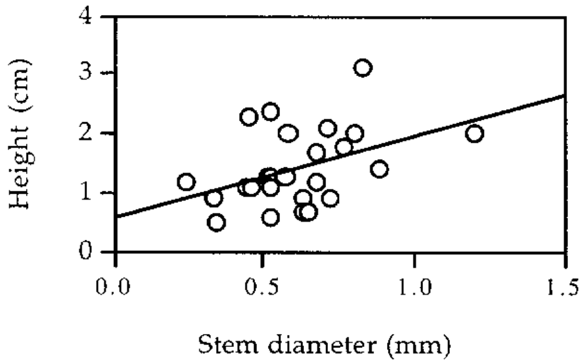


Figure 21: Relationship between *E. victrix* seedling height (cm) and stem diameter (mm) for seedlings measured 23 March 1997 at Marillana (n = 26).

Regression analysis was performed using seedling height and number of leaves in both March and September 1997. Analysis shows a highly significant and positive relationship for the first measurement. Stem height = 0.651 + 0.228 (number of leaves), (r^2 = 0.12 n = 268, P = 0.001***). While a less significant relationship was found on the second date,. Stem height = 3.966 + 0.248 (number of leaves) ($r^2 = 0.051$; n = 111, $P = 0.0171$**) (Figure 22 a and b).

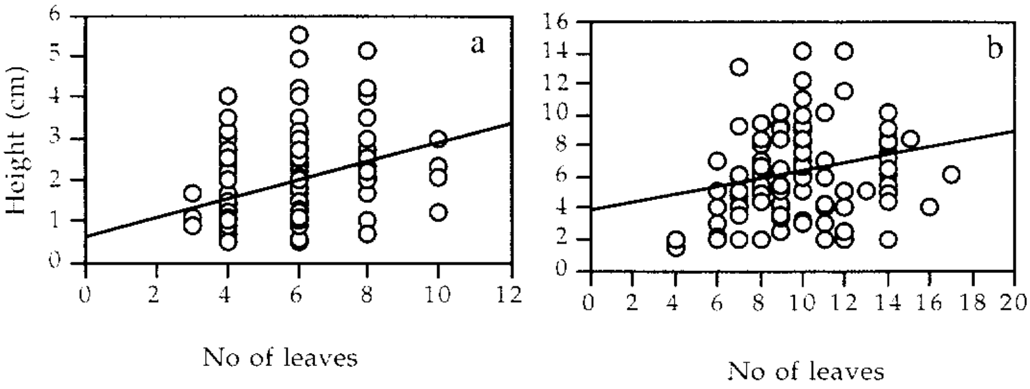


Figure 22: Relationship between seedling height (cm) and number of leaves (a) 23 March, and (b) 21 September 1997 at Marillana station.

A seedling population model was obtained from surviving plants (Figure 23).

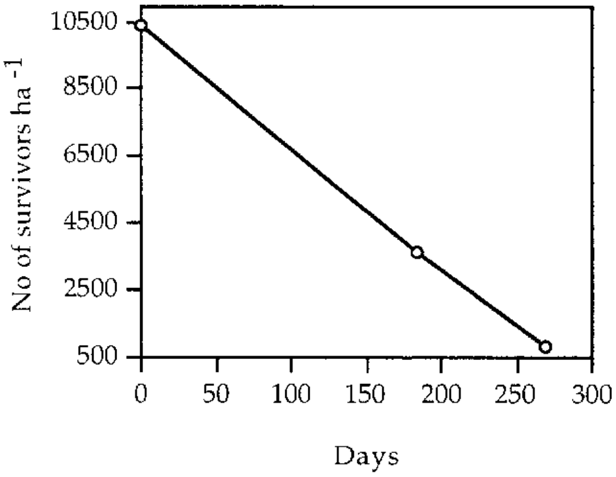


Figure 23: Model survivorship curve for seedlings recorded in Marillana study site during 1997.

These seedlings must have germinated between February and March 1997, when the amount of rainfall received was 257.8 mm. During 1997, a significant establishment rate of 10,346 seedlings per hectare was recorded at the Marillana site (Figure 23). On the final measuring date only 769 seedlings per hectare were found alive.

Population study No. 5. *E. victrix* seedling establishment following fire in a grassland site at Ethel Creek

Introduction

Some frequently inundated parts of the Fortescue River floodplain carry more grass than trees. An area to the northeast of Ethel Creek station has a ground cover community mainly of the swamp grasses *Eriachne flaccida* and *Eriachne benthamii,* with some other herbs (e.g. *Peplidium muelleri*) also contributing ground cover after summer rain. A lightning strike on the adjoining Balfour Downs station, between 20 - 25 February 1996, caused a fire that burnt a part of this grassland. In March 1997, it was observed that a considerable number of *E. victrix* seedlings had become established in the recently burnt area. This site (grassland burnt site) was considered useful to study demography (density, growth and mortality) of *E. victrix*, recruited after such a natural disturbance. This population study allows comparison of demographic factors with other population studies already described for 'natural' recruitment survivorship.

Hypothesis

It was hypothesised that the growth and survival of *E. victrix* seedlings recruited at the disturbed (fire) site would be the same as seedlings recruited at the undisturbed sites.

Methods

On 13 March 1997, 58 seedlings that had established a year earlier were located, tagged and measured. These were of mean height 18 cm and basal shoot diameter of 3 mm, and located in an area of 33 x 13.5 m. Seedling height (cm), stem diameter (mm) at base and number of leaves (counted only in March and July 1997) were recorded. Heights were measured using an extendable carpenter's tape and stem diameters were obtained using digital callipers.

Seedlings were located on a map of the stand and they were remeasured on 9 July and 10 September 1997, and on 12 February and 8 May 1998.

Seedlings were grouped into 12 height classes of 6 cm from 1 to 5.99 cm up to more than 66 cm tall for examining size class distribution. Similarly, 10 stem diameter classes from 1.4 mm up to more than 9.5 mm were used.

Results

The seedlings increased in mean height from 17.86 (SD ± 8.10) cm in March 1997 to 27.70 (SD ± 12.94) cm in June and 29.50 (SD ± 12.97) cm in September 1997. By February 1998, mean height had further increased to 31.01 (SD ± 18.25) cm , but this had decreased to 28.28 (SD ± 14.86) cm by May 1998 (Table 12). A mean growth increment of 1.7 cm per month reflected the amount of rainfall received during 1997. Ninety five percent (n = 55) of seedlings survived 181 days to the September measurement. During February 1998, two seedlings were observed grazed at the base and recorded as dead, but those seedlings had resprouted by May 1998. At the first measurement seedlings had a mean of 29 leaves (SD ± 2.23).

Table 12: Mean dimensions of *E. victrix* seedlings at the grassland burnt site on 5 occasions.

Date	n	Height (cm)± SD	Leaves ± SD
13. 03. 1997	58	17.86± 8.11	29.49 ± 23.58
14. 06. 1997	55	27.70± 12.94	43.65 ± 28.88
10. 09. 1997	55	29.50± 12.97	
12. 02. 1998	53	31.01± 18.25	
08. 05. 1998	55	28.28± 14.86	

The March 1997 height class distribution reveals a normal distribution reflecting the single recruitment event. Thirty six percent (n = 21) of individuals fall in the 12 - 18 cm class and only 5.2% (n = 3) in the 30 - 36 cm height class. In July 1997, 25% (n = 14) of seedlings are in the 30 - 36 cm height class, with 10.7% (n = 6) in the 48 - 54 cm height class. In contrast to March 1997, most had passed through the smaller class (less than 6 cm) leaving only three seedlings. A few seedlings (n = 4) were damaged by cattle between March and September 1997, where a considerable number of seedling leaves were observed as grazed by insects, possibly grasshoppers.

The September 1997 and February 1998 assessments indicate three to four different height class peaks, possibly resulting from herbivory (Figure 24). By September 1997, 24% (n = 14) of seedlings were found in the 12 - 18 cm height class but subsequently in February 1998, 3.7% (n = 2) of individuals occurred in each of the 60 - 66 and more than 66 cm classes.

In May 1998, a few seedlings were again observed to be damaged by cattle. This was reflected in height class distribution with one seedling in the smallest size class. Two peaks were observed in May 1998, 22 (n = 12) and 18% (n = 10) of seedlings in the 24 - 30 and 36 - 42 cm height classes respectively. The overall trend suggests that seedlings are growing, but insect herbivory and damage by cattle slightly affects the increases in height (Figure 24). A similar effect was also observed in the relative growth rate (Figure 25).

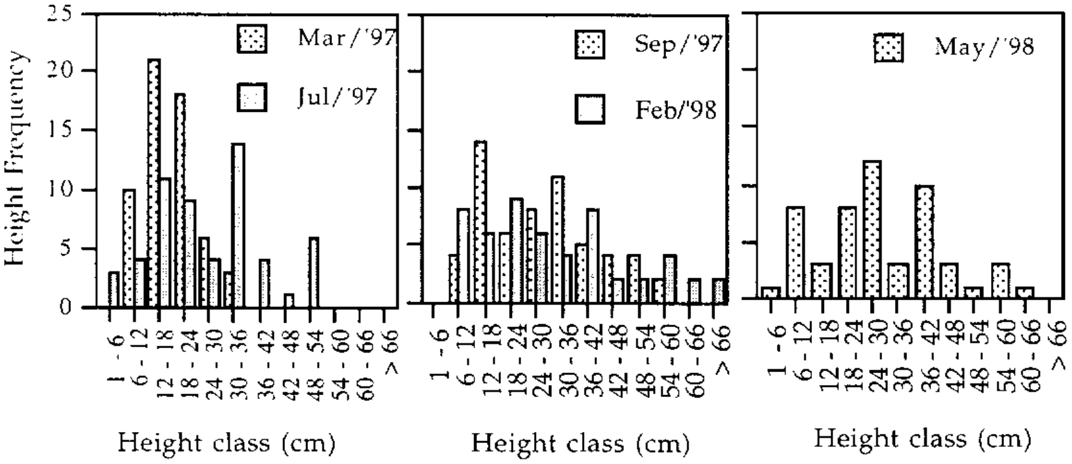


Figure 24: Height class (6 cm classes) distribution of *E. victrix* seedlings at the grassland burnt site at 5 occasions (cm).

Between March and July 1997, mean seedling height increased 9.86 cm, but subsequent means indicate very slow height increments (Table 12). Over the first four measurements (March 1997 to February 1998) an increasing height trend is seen but between the last two measurements, there is a slight decrease in mean height. This was due to damage caused by cattle, grazing effect from insects and lack of soil moisture due to a relatively dry period between February - May 1998, when only 60.2 mm of rain was recorded at Ethel Creek homestead.

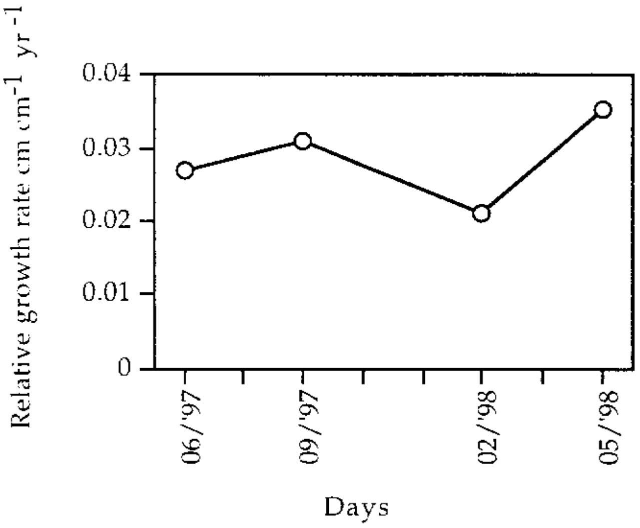


Figure 25: Relative growth rate of *E. victrix* seedlings.

About 12 months after the fire and presumed germination (Figure 26) the linear relationship between height (cm) and stem diameter (mm) is described by: height (cm) = 1.433 + 12.751 (stem diameter) (mm) (r^2 = 0.0068, n= 58, P = 0.0488*).

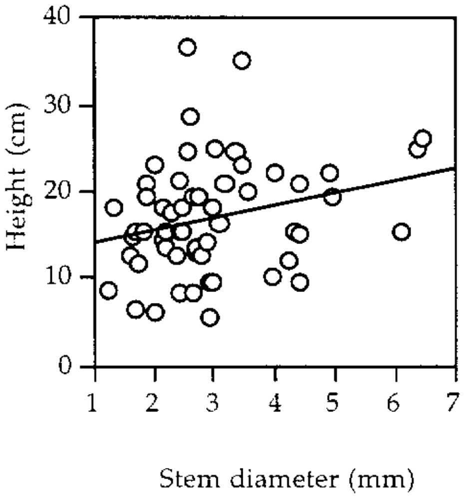


Figure 26: Regression of seedling height (cm) on stem diameter (mm) for March 1997.

Stem diameter size class frequency data for the *E. victrix* seedlings are shown in Figure 27. Mean diameter (mm) varied significantly (F = 28.96, *P* = 0.001***) between measurements. In March 1997 a large number of individuals (37.93% n = 22) fell in the 1.5 - 2.5 (mm) diameter class, with an overall mean of 2.96 mm (SD ± 1.17, n = 58). On the first measurement date the maximum and minimum diameters were 6.47 and 1.22 mm respectively. In May 1998 no stems less than 1.5 mm were recorded and a considerable number of seedlings (42.30% n = 22), were in the 3.5 - 5.5 mm diameter class. However, only 1.92% (n = 1) was recorded in the highest diameter class (more than 9.5 mm). In contrast, by February 1998, 16% (n = 9) of seedlings were recorded in the same diameter class. This was also reflected in mean diameter with 6.74 (SD ± 2.62) and 5.41 (SD ± 1.88) mm diameters recorded in February and May 1998 respectively.

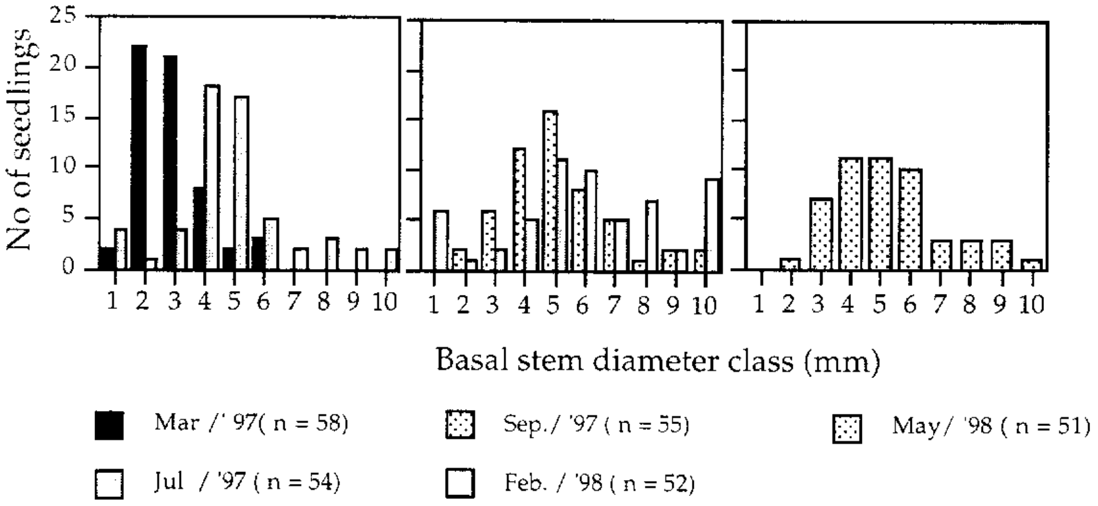


Figure 27: Stem diameter distribution (1 mm classes) of *E. victrix* at grassland burnt site on 5 occasions.

The number of early leaves tends be important for subsequent seedling growth. Initial numbers of leaves (March 1997) and seedling height a year later (May 1998) were positively correlated (Figure 28). This suggests that initial leaf number is a good predictor of seedling growth. The regression relationship is given by, height = 17.866 + 0.402 (leaf number) (r^2 = 0.090; n = 53; *P* = 0.0295*).

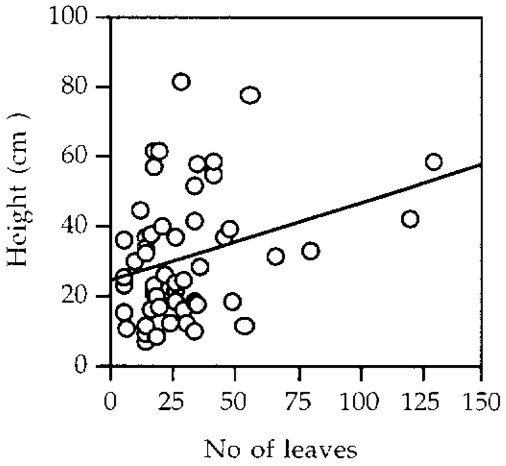


Figure 28: Scatter graph of stem height and total number of *E. victrix* leaves at May 1998.

This seedling population remained relatively stable from 13 March 1997, for slightly more than 14 months (last recorded 08 May 1998), only falling from a density of 1300 plants per/ha in March 1997 to 1, 145 plants per ha in May 1998 (Figure 29).

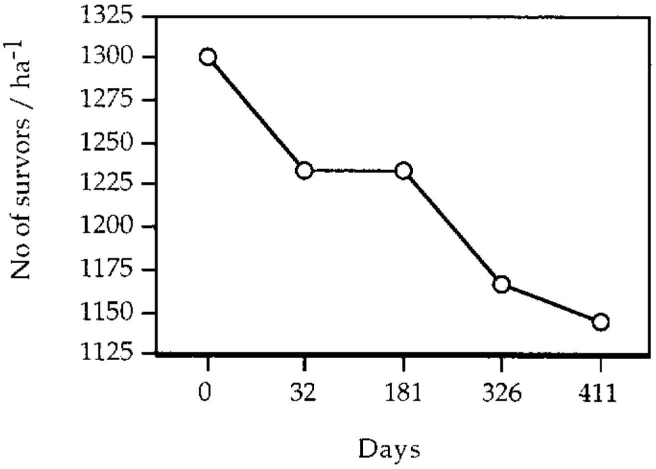


Figure 29: Survivorship curve for *E. victrix* seedling community, recruitment at Ethel Creek (EC40) burnt site.

Discussion

In general, flooding events contribute to higher growth and production on floodplains than on adjacent land (Scott *et al.* 1997). In addition to flooding events, substantial soil moisture and nutrient recharge are important factors for floodplain tree growth and in their absence floodplain tree growth would not be increased (Hughes 1990). The mean annual rainfall of 250 - 450 mm in the Murray Valley is not sufficient for growth of red gum (*E. camaldulensis*) trees, for which flooding in spring or winter is needed (Dexter *et al.* 1986). Trees found in semi-arid floodplains are believed to tolerate flooding events.

The population structure of *E. victrix* stands found on the floodplain of the Fortescue river suggests that medium to large size trees are restricted to discrete, separate, patches. Peaks of different height and stem diameter classes suggest that stands varied in the time of regeneration. Trees with a similar pattern of size class are presumed to have been recruited over similar time periods (sites 1 and 6). Sites with trees more than 11 m tall (sites 1, 2 and 6), presumably have the most favourable soil moisture regimes, relating to soil depth or flooding events. In contrast, stands with trees of less than 2 m mean height reflect more recent recruitment or less favourable soil moisture regimes.

The population structure of *E. victrix* trees at sites 6 and 1 is very similar in both height and diameter, despite those sites being located in different river systems. Although many floodplain trees are established during flooding events, some 30 % of sampled trees aged by Scott *et al.* (1997) are not correlated with flooding events. Other factors such as tributary floods and local slope failures are believed to facilitate additional recruitment events.

A population of *Eucalyptus coolabah* subsp. *arida* observed at Coopers Creek (Roberts 1993) had a single peak and most trees fell in the 7 to 9 m height class. *E. victrix* of the Fortescue valley woodlands is more diverse in status with a considerable range of stands of different apparent origins.

Apparent lack of growth over a period of observation may reflect trees being in a relatively good condition at the start. Both sites 4 and 5 are within 10 m of levee banks of creeks. Apparent growth at these sites may be due to more frequent creek flooding

Persistence of tagged individual saplings for at least two years suggests good survival of established plants. Individuals had developed adequate root systems enabling them to withstand the dry conditions prevailing over spring and summer. This trial has shown that once *E. victrix* reaches a mean height of 80 cm in this environment, subsequent mortality is low.

The sapling height class distribution at September 1995 confirms that this population arose from a single recruitment event. At the first measurement the height data reflected possibly two different recruitment events. Subsequently, (June. 1995) four different peaks were thought to be mainly due to herbivore damage. Two peaks were present among the 35% surviving to the September 1995 measurement. These may have represented differential growth.

Roberts (1993), estimated the age of coolibah found at Cooper Creek using a combination of aerial photography and past rainfall records. He suggested that trees between 4 - 6 m in height may have originated 20 years ago, and a possible recruitment event coincided with above average rainfall received between 1973 and 1975. Fox and O'Connell (1994), studied a set of randomly selected 100 saplings (un-tagged) at RH 2 site. Based on the past 25 years of rainfall data recorded at Roy Hill station, these authors suggest that seedlings with mean height 81.48 (± 27.57) cm may have been recruited in 1988 when more than average rainfall (410 mm) was received at Roy Hill station. In the present study, the poorest five saplings (by height) were selected from September 1995 and mean annual increments were calculated to estimate approximate recruitment years. The best saplings in September 1995 grew from 187.2 cm to 294.2 cm by September 1997. The poorest saplings grew from 36.4 cm to 89.9 cm in height over the same period. Based on the best saplings, (mean annual height change of 53.5 cm) a sapling of 294.2 cm in height would have required 5.5 years to September 1997. Similarly, if the poorest rate had been followed, the mean annual height change measured is 26.8 cm, and saplings of 89.9 would have taken 3.4 years to grow. Therefore an estimate of origin for this population is between 1992 and 1994. If the best saplings measured in September 1995, had grown at the poorest rate, then the time required to attain this height would have been 2 years, i.e. from 1993.

Height and stem diameter growth appear to be strongly affected by topographic position and the gilgaied landscape. Saplings on the edge of the gilgai grow larger than in the gilgai. It is possible that saplings in the gilgai are more frequently flooded than those on higher ground. Pounding of rain in the depression may also have an effect on sapling growth within gilgai. As time passes, competition from the well-established saplings growing on the edge and top of the gilgai may further curtail growth. In a few years time these saplings will come under competition pressure and may be further naturally thinned so that the spacing between them could become greater.

The time of first flowering varies between species and within individuals in a species of eucalypt. Gill (1981) observed *E. regnans* produced seeds when they were 15 to 20 years old. Similarly Abbott and Loneragan (1986) found *E. marginata* saplings attain reproductive stage when 1.5 m tall. In May 1998, eight of the tagged sapling population were observed to have produced fruits in the preceding summer. These individuals had a mean height of 2.50 m and stem diameter of 48.90 mm.

Early mortality rate in *E. victrix* is similar to other eucalypts (Stoneman 1992). Mortality of newly recruited seedlings was high in the six months following germination. Unpredictable and sporadic rainfall, competition and subsequent dry conditions possibly play a major roll in seedling mortality in the coolibah woodland (Wellington and Noble 1985a). It is also believed that competition between grasses and *E. victrix* seedlings for water also plays a major role (Anderson 1967). Insect damage also appears to be an important factor in increasing mortality. This pilot study shows that the early summer months after seedlings are recruited is the most critical period for survival of *E. victrix* seedlings. Survivorship curves applied to established *E. victrix* seedlings follow a type III Deevey (1947) survivorship curve.

It was observed in 1997 that a considerable number of seedlings had germinated on a thick mat of leaf litter. These died before roots reached the surface soil. It was also observed that seedlings germinated on a wet surface, sealed by a thin layer of clay soil formed after dispersed clay had washed down from higher ground. On that washed clay deposit, a considerable number of *E. victrix* seedlings had germinated with a mean of 2 - 4 leaves. The seedlings appeared unhealthy and probably died early in summer due to high temperatures.

Generally, recruitment events involving *E. victrix* seedlings occur during mid-late summer when the ground is moist and seed available. This is often February to the latter part of March. Recruitment mainly depends on the extent of summer rainfall and cyclonic events generally pass through the Pilbara region between December and February. Relatively poor rainfall during January - July of 1996 coincided with no observed recruitment during that period.

Seedling establishment is a very important stage for eucalypts. The survival rate is very low during the first few years (Stoneman 1992). Seedling mortality is attributed to three important factors: firstly, limited root penetration during summer months (Kummerow *et al.* 1985); secondly, competition for soil moisture in the root zone with neighbouring species (mainly grasses) during the early stage of summer (Huiquan and Turvey 1994); and thirdly, the combined effects of drought and herbivory (Mills 1983). In addition, natural disturbance and catastrophic events such as wind throw and fire also play a major role in increasing juvenile seedling mortality (Enright and Lamont 1989, Taylor and Aarssen 1989).

Yates (1995) found that large numbers of *Eucalyptus salmonophloia* seedlings were recruited in previously burnt, flooded and storm-damaged sites when compared with undisturbed sites. Seedling recruitment of *E. victrix* occurs after flooding events in the coolibah woodland. However, seedlings rarely persist beyond the cotyledon or 4-6 leaf stage. In mallee eucalypts, Wellington and Noble (1985a) found seedling mortality high as a result of prolonged drought and high temperatures during the first summer.

The establishment of uniform-size seedlings in Marillana during early 1995 and 1997 indicates that seedling recruitment can only occur after sufficient soil moisture becomes available.

Seedling recruitment confirms viable seed production. Heavy mortality suggests that seedlings need exceptional climatic conditions to survive. Extant *E. victrix* trees have considerable demand on residual surface soil moisture supply after summer, leaving new seedlings with little moisture and relatively exposed to high temperatures. Seedling survivorship may be enhanced through gaps created by the death of mature trees (Wellington 1984, Wellington and Noble 1985b).

At the burnt site, greater seedling establishment (1,301/ ha) and survival (1,144.8/ ha) probably resulted from the fire effect. Fire possibly eliminated competing roots of pre-existent trees of *E. victrix* and *Acacia ancistrocarpa*. Also the roots of grass species were probably temporarily damaged. Seedling mortality is generally lower on ash beds than it is when seedlings are germinated on beds without ash (O'Dowd and Gill 1984, Burrows *et al.* 1990). Surface ash made a suitable environment for the newly recruited seedlings to survive over a period of more than 12 months. Fire also triggered germination of a large number of *Acacia ancistrocarpa*. During September 1997 it was observed that the burnt grass *Eriachne benthamii* had produced new leaves following above average rainfall received between January and September 1997 (356 mm recorded at Ethel Creek homestead). Most of this (90%) fell between January and May 1997.

The survival rate of *E. victrix* seedlings that germinated after fire appears to have been much higher than those germinated in unburnt areas of the floodplain. The main difference may have been due to the presence of better established root systems (Wellington 1984). Also the fire killed a mature *E. victrix* and a few *A. ancistrocarpa*. Further, reduction in competition (Moore and Williams 1976) may have contributed to the survival of newly recruited seedlings at the beginning, compared with seedlings recruited in undisturbed sites. Particularly, during the summer competition for water from mature trees would have been much reduced as the fire burnt back the perennial grasses in the vicinity to ground level.

During May 1998, it was observed that 18% of measured seedlings had been grazed and damaged by cattle. Leaves were also grazed by insects. Death of seedlings and reduced height was mainly due to cattle interference. Several types of grasshoppers are believed to graze seedlings and trees in this area. For example *Nomadacris guttulosa* and *Goniaea australasiae* (Family - Acrididae). These were identified at Jackson's Bore Paddock, in Ethel Creek station.

In conclusion, continuous moisture appears very important to trigger germination of *E. victrix* seeds as well as the subsequent growth of seedlings. Death of newly recruited seedlings during early summer is probably due to high temperature, drought and competitive interactions from neighbouring grasses and root competition from mature *E. victrix* trees. Once seedlings have survived the first summer, they are more resilient to harsh conditions in following years.

Further, it appears that fire created a suitable condition for *E. victrix* seedlings to establish by providing nutrients, creating reduced root competition and by killing mature trees and creating gaps, for seedlings to get enough light

(Loneragan and Loneragan 1964). In addition, fire localises nutrients ('ash bed effect') from burnt materials (Loneragan and Loneragan 1964). Added nutrients may allow seedlings to grow faster and healthier. After fire most herbs and some shrubs/small trees are burnt and thus will not compete for soil moisture and nutrients. The mean height of surviving seedlings is increasing in trend, but their height may be affected when competition for water and nutrients sets in from *A. ancistrocarpa* seedlings which also germinated after the fire.

CHAPTER 3

Morphological, physiological and anatomical adaptations to waterlogging by seedlings of *E. victrix*

Introduction

When soil becomes waterlogged, the air within the soil is replaced by water. Since diffusion of oxygen in water is four orders of magnitude slower than in air, the continued oxygen demand of soil organisms and plant roots rapidly depletes the oxygen content of waterlogged soil (Dionigi *et al.* 1985). Several woody angiosperms produce adventitious roots from the inundated part of the plant. This adaptation may contribute to survival in the waterlogged condition (Hook 1984, Kozlowski 1984a, Kozlowski *et al.* 1991). This change is attributed to endogenous hormones (Yamamoto *et al.* 1995).

It is believed that there is an anatomical relationship between formation of lenticels and production of adventitious roots (Newsome *et al.* 1982) but Angeles *et al.* (1986) report only a few adventitious roots emerge through lenticels in flooded *Ulmus americana* seedlings. Adventitious roots differ from normal lateral roots in having relatively large cells and extensive intercellular spaces. The vascular cylinder and endodermis are similar in both types of root (Kozlowski 1984a).

Hypertrophy of the stem is another morphological change associated with exposure to flooding. This adaptation is reported in *Alnus japonica* and is partly attributed to the regulatory effects of endogenous hormones (Yamamoto *et al.* 1995). In conifer seedlings, it is associated with substantial cambial activity, wood production and increased bark thickness (Yamamoto and Kozlowski 1987a, b; Yamamoto *et al.* 1987).

The large Australian genus *Eucalyptus* has species adapted to a wide range of climatic and edaphic conditions (Goor and Barney 1968). Vernacular names often indicate tolerance of environments subject to flooding: *e. g.* flooded gum, *E. grandis* Hill ex Maiden and *E. rudis* Endl.; swamp gum *E. camphora* R. T. Baker and *E. ovata* Labill.; swamp mahogany *E. robusta* Sm. These are all species that can withstand some degree of inundation (Ladiges and Kelso 1977, Clemens and Pearson 1977, Kozlowski *et al.* 1991). The river red gum (*E. camaldulensis* Dehnh.), of south-eastern Australia, is dependant on periodic flooding. Seed germinates on flooded areas following flood recession (Parsons *et al.* 1991). The coolibah species *E. microtheca* is an important plantation tree grown with flood irrigation in the Sudan (Ahmed 1977). The taxon *E. victrix* may comprise a part of the earlier entity known as *E. microtheca* (Doran and Boland 1984). Tolerance to flooding has been examined in *E. robusta* (Clemens and Pearson 1977); *E. robusta, E. grandis* and *E. saligna* Smith (Clemens *et al.* 1978); *E. ovata* and *E. viminalis* Labill. (Ladiges and Kelso 1977); and *E. marginata* Sm. (Davison and Tay 1985).

Tree species that occur in flood plain environments experience exposure to flooding that may be regular or irregular, and of varied duration and frequency. *E. victrix* forms open, grassy woodlands in the flood plain of the Fortescue River valley (Xin *et al.* 1996). This area is subject to summer flooding from cyclones or heavy thunder storm activity between January and March. Depending on the topography of the woodland, flood water may remain for a month or more. The present study was undertaken to examine aspects of tolerance to flooding in *E. victrix* seedlings using plants of different ages from germination.

Hypothesis

Growth and gas exchange measurements on seedlings of *E. victrix* (different aged) will not affected by prolonged flooding.

Methods

Seed extracted from mature fruit capsules of *E. victrix* (collected in February 1995) from the coolibah woodland of the Fortescue near Ethel Creek (lat. 22° 54'S, long. 120° 10'E), were stored in a sealed jar at laboratory temperature (about 21°C). Aliquots of seed were sown onto sterilised coarse sand on 1. 8. 1995 and 3. 9. 1995.

Pots of 13 cm in diameter were filled with coolibah woodland soil (red clay loam, pH 7) and the bottom openings sealed with plastic draining tapes. Seedlings were transplanted into pots at the 2-4 leaf stage, at about three weeks (23. 8. 1995 and 21. 9. 95) from sowing. Plants were maintained in a shade house until 18.12.1995 when they were placed in full sunlight. After five days acclimatisation, flooding treatment commenced (23. 12. 1995). The plants were 13- or 17-week seedlings at the start of flooding, with mean heights of 14.1 and 19.0 cm respectively. Fibreglass tanks of 2.5 x 0.5 x 0.5 m were filled with rainwater to a depth of 1 cm above the pot soil level. (Twelve plants aged 13-weeks and 8 plants of 17-weeks were used). Rainwater was topped up daily. Control plants were placed adjacent to the tanks and these were maintained in a freely draining condition. These pots were watered to excess three times a week (4 plants). All plants were in full sun.

Further seed was sown and seedlings prepared as before, to give 4- and 8-week seedlings. On 7. 3. 1996 representative plants of these sets were selected for flooding treatment or control as described above.

Observations were made of seedling height, leaf number, and leaf dimensions. New leaf emergence and leaf death were noted. Any changes in seedling morphology, particularly stem swelling, leaf colour changes and development of adventitious roots were recorded.

Gas exchange measurement

Gas exchange measurements were made on the 13- and 17- week plants using individual leaves sampled from each plant commencing 8 days after the start of flooding and continuing for 6 weeks (31. 12. 1995 - 2. 2. 1996). Simultaneous measurements of internal CO_2 concentration (ci); photosynthetic CO_2 assimilation giving net photosynthesis (Pn); leaf conductance to water vapour (stomatal conductance gs) and transpiration rate (E) were made under ambient conditions. Equipment used consisted of a portable leaf chamber (Parkinson PLC-031 3B) and infra-red gas analyser (IRGA) operated in the differential mode (model LCA-3, Analytical Development Co. Ltd., Hoddesdon, Hertfordshire, UK). Measurements were taken consistently at 1200 - 1300 hours.

All plants were harvested 32 weeks after flooding of the 13- and 17-week sets and carefully removed from pots. Fresh weights of root and shoot were obtained. Plants were then put in separately labelled paper bags and dry weights obtained after 24 hr at 105°C.

Representative inundated stem sections of 4- and 8-week old seedlings (1 cm from the lignotuber) and roots (2 cm from the soil surface) were taken for observation. These were preserved in AA solution (formaldehyde/acetic acid/ethyl alcohol 5/5/90 mL) immediately after removal from the water-logged condition. Before sectioning, specimens were rinsed in 50% alcohol. Samples were sectioned transversely using a double edged blade. Sections were mounted in glycerol on a clear glass slide and observed under a light microscope. Permanent sections were made after staining with safranine-fast green solution and mounted in Diatex.

Analysis of variance was used to examine whether flooded or control sets differed in harvest values.

Statistical analyses

Data were analysed using Super ANOVA software program (Abacus Concepts, Berkley, California) for one-way ANOVA. Residual plots of each ANOVA were obtained to examine homogeneity of varience. Based on redidual plot, data were transformed to log or square root as appropriate and reanalysed. The data presented here are of uniform means.

Results

Two seedlings of the 4-week set died after 5 months of flooding, all others survived the experimental period of 32 weeks.

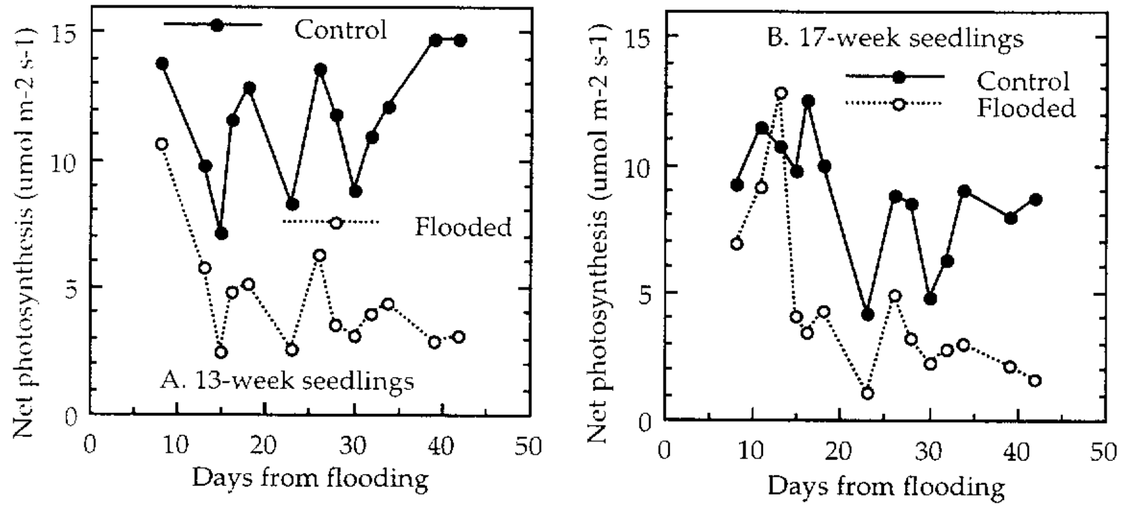


Figure 30: Mean net photosynthesis for 6 wk following flooding on 13- and 17-wk seedlings of *E. victrix* with unflooded controls. Values are means of four leaves for control plants and eight leaves from flooded plants.

The plotted Pn (net photosynthetic rate) of 13-week control plants fluctuates considerably but remains above 7 μmol m^{-2} s^{-1} during the observation period. In contrast, Pn of flooded plants declines to less than 5 μmol m^{-2} s^{-1} after two weeks flooding and remains below 7 μmol m^{-2} s^{-1} thereafter (Figure 30). After waterlogging was imposed the older plants show an initial increase in Pn but values for flooded plants show a sharp decline after 12 days so that by 15 days both flooded sets have similar Pn and these are consistently lower than control plants over the rest of the observation period.

The older control plants show a declining tendency in Pn. Their consistently lower values than those of the younger set, probably that pot resources were becoming scarce.

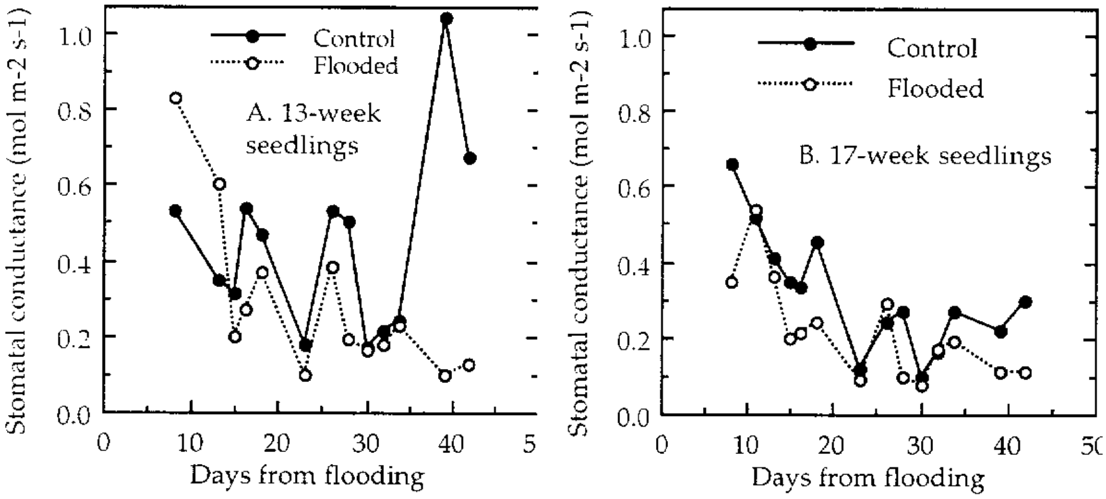


Figure 31: Mean stomatal conductance for 6 wk following flooding on 13- and 17- wk seedlings of *E. victrix* with unflooded controls.

Trends in gs (stomatal conductance) are generally similar to those of Pn, showing a decline in younger flooded plants sooner than in older ones (Figure 31). Control plant gs values also gradually decrease during the study period, apart from a major (unexplained) fluctuation at 40 days in the 13 week set. Fifteen days after the imposition of flooding most values for flooded plants are below those of the corresponding control and remain less.

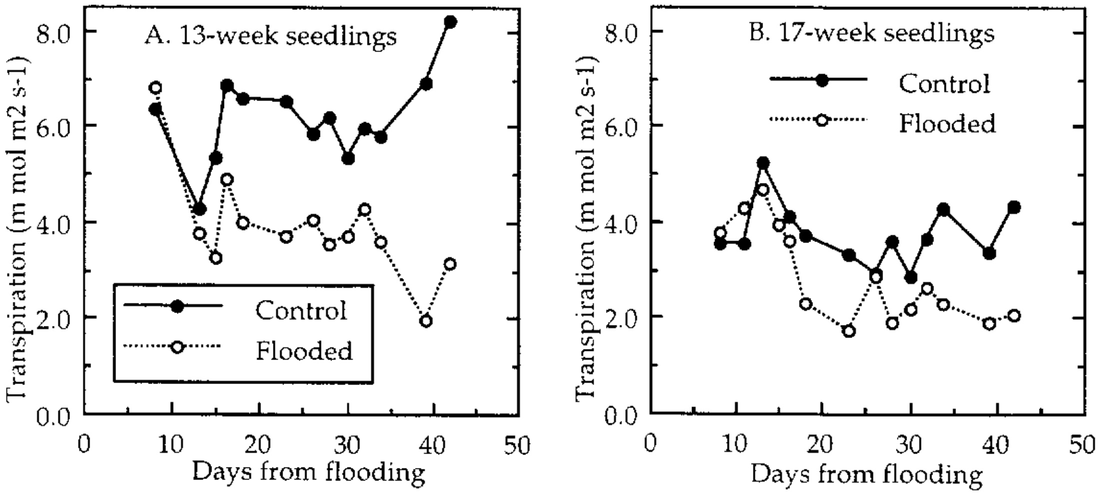


Figure 32: Mean transpiration rate for 6 wk following flooding on 13- and 17- wk seedlings of *E. victrix* with unflooded controls.

Transpiration rates of both 13- and 17- week sets are similar for control and flooded plants at the first measurement (Figure 32). There is a clear difference with age in that the 13-week plants have higher rates throughout. After 15 days, flooded seedlings have consistently lower transpiration rates than the corresponding controls.

Leaf colour changed from 16 days after waterlogging. Leaves initially became reddish-brown, some became yellowish after 32 days. By 47 days from flooding, submerged stems had begun to show splitting in the 17-week set. Adventitious root development was observed from 42 days in the 13 week set and from 62 days in the 17-week plants. Mean leaf areas (mm^2) of the 17-week plants at harvest were: control 789 (SD ± 424); flooded 1063 (SD ± 427). Flooded seedlings shed an average of two leaves each. New leaf formation appeared to be continuous in both treated and untreated plants but was more prolific in flooded plants.

In all four seedling age sets the mean shoot height at harvest does not differ significantly between control and flooded seedlings (Tables 13 and 14). There is no significant difference in dry shoot weights even though 13-week flooded seedlings have almost twice the mean weight of the control (Table 13).

Table 13: Harvest details of 4- and 8- week old *Eucalyptus victrix* seedlings after flooding.

Treatment	Set (age in wk)	n	Shoot height (cm)	Shoot dry weight (g)	Root length (cm)	Root dry weight (g)	Stem diameter (mm)	No. of adventitious roots
			Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Flooded	4	11	12.91 (0.95)	0.80 (0.08)	26.40 (1.80)	0.41 (0.70)	3.16 (0.37)	14.72 (1.01)
Unflooded	4	4	10.88 (0.58)	0.59 (0.05)	57.40 (5.70)	1.01 (0.07)	2.20 (0.13)	0.00 (0.00)
Flooded	8	12	21.90 (1.34)	2.42 (0.29)	23.26 (6.22)	0.94 (0.19)	5.68 (0.33)	13.41 (1.16)
Unflooded	8	4	21.77 (5.11)	1.83 (0.45)	40.50 (7.00)	2.54 (1.40)	3.70 (0.56)	0.00 (0.00)

ANOVA table

Contrast	Shoot height (cm)				Shoot dry weight (g)			Root length (cm)			Root dry weight (g)			Stem diameter (mm)			No. of adventitious roots		
	df	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*	ms	F	*P*	MS	F	*P*
Flooding	1	6.79	0.1	NS	0.9	1.7	NS	3454.3	70.7	***	7.2	17.3	***	12.8	10.3	**	1174.7	69.0	***
Age	1	585.7	24.0	***	12.1	22.3	***	593.6	12.1	**	6.2	14.8	***	23.8	19.2	***	2.54	0.1	NS
Flooding x Age	1	5.39	0.2	NS	0.2	0.3	NS	282.2	5.7	*	1.5	3.5	NS	1.52	1.2	NS	2.54	0.1	NS
Error	27	656.4	24.31		0.5			48.8			0.4								

P* <0.05; ***P*<0.005; * *P*< 0.001; NS= not significant

Flooding resulted in the 4- and 8-week seedlings differing significantly (*P* =0.0001) in root length, root mass, stem diameter and number of adventitious roots (Table 13). There is no significant difference in shoot height or dry mass. A significant interaction between flooding condition and seedling age is observed in root length.

Harvest data of 13- and 17-week seedlings reveal flooding is associated with significant differences (*P* = 0.0001) in root length, stem diameter and number of adventitious roots (Table 14). A significant interaction between flooding condition and seedling age is observed in shoot height and root length.

At harvest, all original root systems on waterlogged plants were soft and black, in stark contrast to the white-cream coloured adventitious roots (Figures 33 and 34).

Table 14: Harvest details of 13- and 17-week old *Eucalyptus victrix* seedlings.

Treatment	Set (age in wk)	n	Shoot height (cm)	Shoot dry weight (g)	Root length (cm)	Root dry weight (g)	Stem diameter (mm)	No. of adventitious roots
			Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Flooding	13	12	16.66 (0.99)	1.54 (0.21)	20.56 (2.28)	3.02 (0.75)	4.70 (0.23)	10.00 (1.04)
Unflooded	13	4	16.20 (0.75)	0.84 (0.17)	38.75 (1.63)	2.33 (0.75)	3.05 (0.64)	0.00 (0.00)
Flooded	17	7	22.09 (2.22)	4.71 (0.39)	27.19 (1.02)	8.17 (1.50)	7.40 (0.78)	10.14 (1.40)
Unflooded	17	4	21.05 (1.80)	4.41 (0.31)	27.78 (3.10)	4.37 (0.68)	4.31 (0.29)	0.00 (0.00)

ANOVA table

Contrast	Shoot height (cm)				Shoot dry weight (g)			Root length (cm)			Root dry weight (g)			Stem diameter (mm)			No. of adventitious roots		
	df	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*	MS	F	*P*
Flooding	1	3.0	0.1	NS	1.35	2.21	NS	568.7	15.9	***	27.73	3.5	NS	31.0	18.4	***	558.7	56.64	***
Age	1	145.4	8.7	**	62.18	101.1	***	10.8	0.3	NS	70.8	9.0	**	21.4	12.7	**	0.02	0.00	NS
Flooding x Age	1	0.45	0.02	*	0.22	0.3	NS	354.4	9.9	**	13.2	1.6	NS	2.8	1.7	NS	0.02	0.00	NS
Error		2316.5			0.6			35.6			7.8			1.68			9.8		

*P <0.05; ** P<0.01; *** P< 0.001; NS= not significant

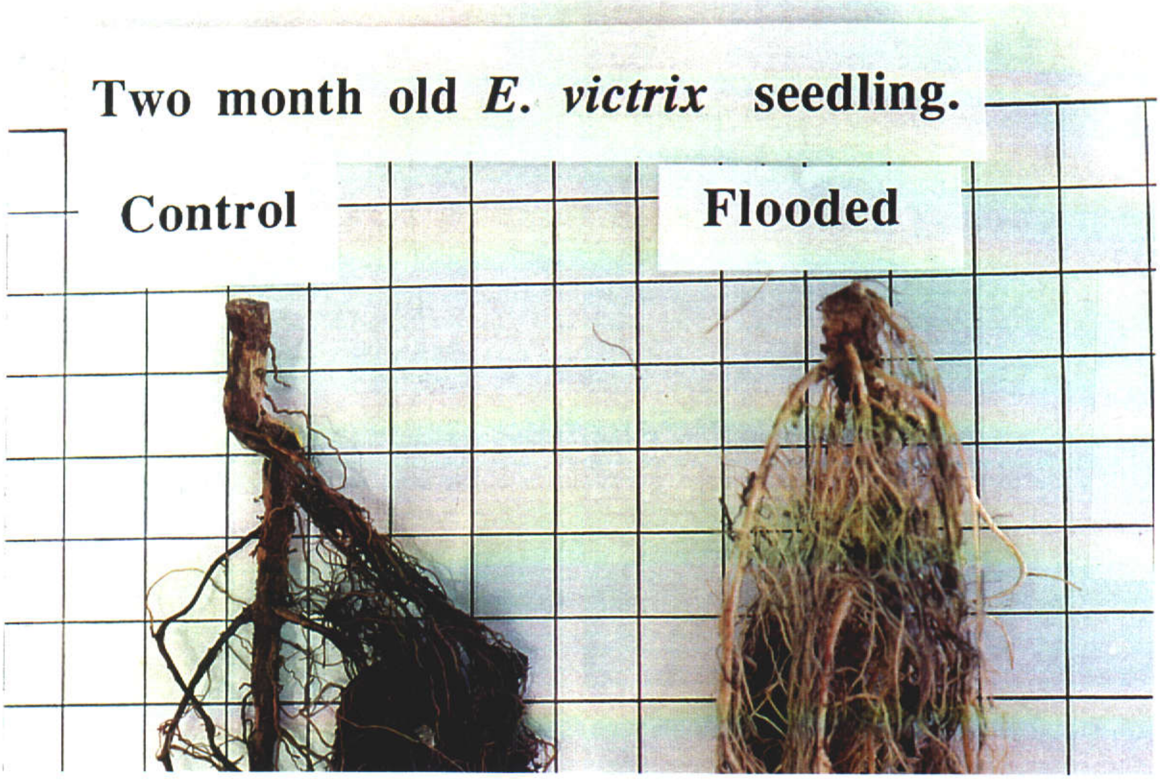


Figure 33: Note the differences in control and flooded *E. victrix* seedlings. Adventitious roots formed on flooded *E. victrix* seedlings. Photo was taken at the end of the experiment. [Grid is 1 x 1 cm].

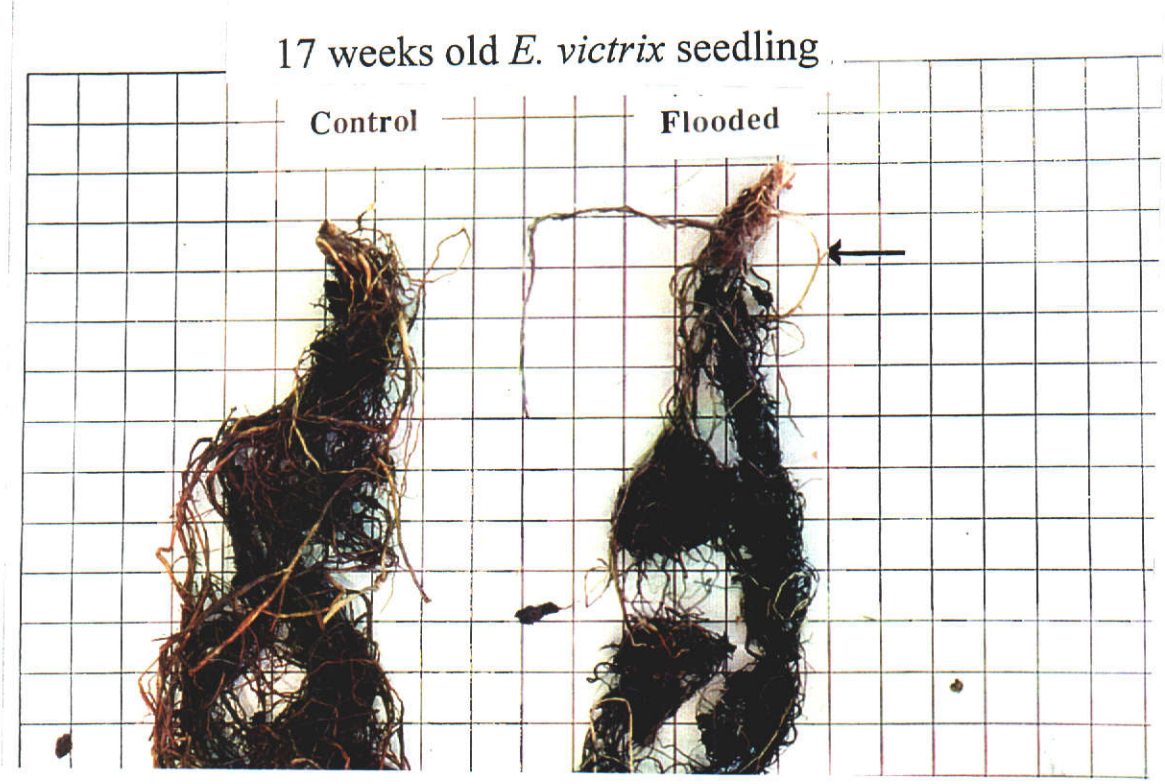


Figure 34: Note the difference in control and flooded *E. victrix* seedlings. Just above the dead roots, adventitious roots were formed in the three month old *E. victrix* flooded seedlings. Arrow indicates the adventitious root. [Grid is 1 x 1 cm].

Flooding has greatest effect on original seedling roots. In both the older sets the roots of flooded seedlings were black and decaying by the end of the experiment. Just above the dead roots, prolific white adventitious roots were clearly observed in the 8 weeks old seedlings (Figure 33).

At the inundated stem base abnormal development (hypertrophy) results in cracking and some lenticel development. In contrast, no such morphological change was observed in unflooded seedlings. Examination of slides indicated extensive development of aerenchymous tissue and superficial bark lesions in flooded material.

Discussion

The process of adaptation to flooding by a single plant may require some time and transplanting shock is difficult to quantify (Megonigal and Day 1992). The use of seedlings of different ages clearly minimises initial root and shoot imbalances. The younger sets were of necessity not as well buffered to cope with flooding as seen in the lower root weights than shoot weights in 4- and 8-week seedlings compared with older sets. Established potted transplants of *E. victrix* appear to require 10-15 days for physiological adjustments to operate. Younger, 14 cm height (13-week plants) are more sensitive than 19 cm height (17-week plants) in this respect. The relatively small mean height changes for all seedlings suggests that pot volume probably limited the expression of foliage material in the present study, whether plants were flooded or not.

Flooding may lead to much of the pre-existing root system being replaced with a new, morphologically distinct system (Hook 1984). Whether flood tolerant species can make continuous adjustments in root systems in response to periodical flooding is an interesting issue. Adventitious root development and intercellular air spaces are common responses to flooding. Adventitious roots are believed to confer tolerance to flooding (Sena Gomes and Kozlowski 1980a, Kozlowski *et al.* 1991). Initiation of these roots is correlated with growth improvement in *E. camaldulensis* (Sena Gomes and

Kozlowski 1980a). Interestingly, the adventitious root material floated above the soil in the water tanks and it is unclear whether this would be a useful adaptation in the field. Flooding in the Fortescue River valley is accompanied by considerable soil movement and it is possible that receding floodwaters could drop silt/clay material over any surface roots developed during a flood.

More detailed physiological analyses may have shown a change in transpiration rate in older flooded seedlings closer to the time at which adventitious roots had become visible as seen in 4-month old *Fraxinus pennsylvanica* flooded seedlings (Sena Gomes and Kozlowski 1980b). The production of adventitious roots is mainly due to flooding injury but may also be associated with ethylene production. Production of ethylene in unflooded plants has been associated with leaf epinasty (Denny and Miller 1935), hypertrophy of lenticels and cortex and formation of adventitious roots (Abeles 1973), and stem thickening (Zimmermann and Hitchcock 1933). Artificial application of ethylene releasing chemicals produces symptoms similar to those of flooding (Abeles 1973, Kawase 1974). Increased stem diameter may follow absorption of water by the bark. In *Eucalyptus globulus* 10 days after flooding, the submerged portion of the stem had swollen (Sena Gomes and Kozlowski 1980a). Similar observations apply to *E. viminalis, E. ovata* and *E. robusta* (Ladiges and Kelso 1977, Clemens and Pearson 1977).

Plant reactions to waterlogging vary with the duration, season, and tolerance to the stress (Ranney and Bir 1994). Root to shoot ratios may be expected to decrease in response to prolonged flooding (Megonigal and Day 1992). Although flooding time was equally long for all aged seedlings tested, *E. victrix,* root/shoot ratios increased in the 17 weeks and decreased in response to flooding in all other measurements. It was observed that root length was reduced by flooding in all except the oldest seedlings. In flooded conditions the soil becomes oxygen limited, in turn limiting physiological activity. Water and nutrient supplies through roots are reduced and the normal hormonal balance governing root shoot development can be disturbed (Kozlowski 1982). Flooded plants had a greater leaf area than control plants, at least in older plants, and leaf production did not appear inhibited by flooding. I hypothesised that a high seedling root/shoot ratio in *E. victrix* is an adaptation to drought. Despite the habitat of interest being a floodplain, long dry periods occur each spring and longer droughts, with no flooding, are not uncommon. There is probably a change-over step when seedlings are large enough to permit sufficient bulk of new roots to replace those killed by the effects of flooding and this is associated with attained plant size at the onset of flooding. Alternatively, as all flooded plants had similar mean numbers of adventitious roots, perhaps the process simply requires more time in younger plants.

Observation suggests that seed dispersal of *E. victrix* occurs mainly in hot weather in summer (February to March), coincident with the greatest likelihood of rain (Chapter 2). When capsules are ripe they dry rapidly, shedding the light weight seed that may blow some distance away. Germination is rapid at an optimum temperature of ~ 35-40°C (Doran and Boland 1984) and is mainly effective in seedling production when seed falls onto moist sites just drying out from summer rain or flooding. The possibility of further flooding is high and this may lead to seedling submergence. The interest in this study was whether small seedlings of *E. victrix* can survive flooding. Field evidence suggests that established plants of 1-2 m can survive flooding but also that large numbers of summer germinating seedlings do not survive the following dry spring. The evidence obtained suggests that seedlings of this species are remarkably tolerant of flooding although total immersion has not been trialed.

CHAPTER 4

Comparison of flooding tolerance of three *Eucalyptus* species from the semi-arid Pilbara District of Western Australia

Introduction

When plants are exposed to waterlogging the gradual depletion of soil oxygen induces many physiological and morphological changes in the plant (Kozlowski 1984b). Within the large genus *Eucalyptus*, species of the sub-genus Monocalyptus are less water and frost tolerant than are Symphyomyrtus species (Noble 1989, Davidson and Reid 1987). No Monocalyptus species have been shown to tolerate waterlogged conditions (van der Moezel and Bell 1990, McComb *et al.* 1989, Bell *et al.* 1994), although, of two south-west WA Monocalyptus, *E. marginata* (jarrah) is very intolerant to waterlogging (Davison and Tay 1985), whereas *E. patens* is often found in low-lying areas (Bell and Williams 1997). Species intolerant of waterlogging generally show no morphological changes and no recovery of gas exchange during exposure to the waterlogged condition (Tang and Kozlowski 1982). Species tolerant of waterlogging often show reduced stomatal conductance and transpiration but tend to recover immediately after adventitious roots are formed (Gomes and Kozlowski 1980a, b).

Early stomatal closure is the major physiological change when a plant is exposed to waterlogging (Gomes and Kozlowski 1980a). Other important adaptations are a reduction in the rate of photosynthesis rate (Regehr *et al.* 1975) and a decrease in absorption of water and minerals (Kramer 1969). Stomatal closure and opening vary between species. In *E. camaldulensis*, stomata reopen after 35 days of waterlogging (Gomes and Kozlowski 1980a); in *Quercus macrocarpa* they reopen after about 30 days waterlogging (Tang and Kozlowski

1982), whereas in *Nothofagus solandri* and *N. menziesii,* stomata do not reopen during the waterlogging period (Sun *et al.* 1995).

Clemens *et al.* (1978) rank the following three *Eucalyptus* on their tolerance to inundation: *E. grandis* > *E. robusta* > *E. saligna.* Flooding reduces the growth of *E. globulus* more than that of *E. camaldulensis* (Gomes and Kozlowski 1980a). Seedlings of both produce abundant adventitious roots that originate near the taproot and original lateral roots, but only *E. camaldulensis* produces adventitious roots on the submerged portion of the stems. Ladiges and Kelso (1977) compared two populations of *E. viminalis* and one of *E. ovata. E. viminalis* grew faster than *E. ovata* in non - saturated soil but height was reduced when they were exposed to waterlogging.

Symphyomyrtus species that occur on or adjacent to the Fortescue floodplain, besides *E. victrix,* are *E. camaldulensis* var. *obtusa* Blakely and *E. leucophloia* Brooker. Other important species are *E. aspera.* (subgenus Blakella), *E. terminalis* F. Muell. and *E. deserticola* Carr & Carr (subgenus Corymbia).

The present experiment compares three Pilbara eucalyptus (*E. victrix, E. terminalis* and *E. leucophloia*) that differ in ecological habitat. *E. victrix* is confined to typical floodplain sites; *E. terminalis* occurs on river banks but is also scattered on hillsides, whereas *E. leucophloia* occurs mostly on stony hills.

Hypothesis

Seedlings of non-floodplain *Eucalyptus* species are less tolerant to flooding than the typical flood plain species *E. victrix* .

Method

Seeds of *E. victrix* (smooth - barked coolibah), *E. terminalis* (desert blood wood) and *E. leucophloia* (migum/snappygum), were collected from sites near Newman, Pilbara, Western Australia on 27 March 1997. Air dried, but uncleaned seeds were stored in air tight bottles and kept at room temperature until use. On 25 July 1997 seeds were sown on sterilised coarse sand in seedling trays at the Field Trial Area of Curtin University. On 15th of August, 50 uniform sized (5 - 6 cm high) seedlings from each species, were transplanted into black, round, cylindrical pots (150 mm high and 80 mm wide), containing clay soil collected from coolibah woodland. All pots were kept in a glass house and water was added 3 - 4 times a week. On 21 January 1998 (to simulate the natural condition) uniform size seedlings (29 seedlings of *E. victrix* and *E. leucophloia* and 35 seedlings of *E. terminalis*) were selected. Roots of all three of the species had penetrated through the basal holes. For uniformity these plants were removed carefully and roots were trimmed. The seedlings were then placed in the middle of plastic pots (140 mm high and 130 mm wide) and any gaps were filled with coolibah woodland soil, as used in the previous experiment (Chapter 3). Pots were moistened and left in the glass house for one week. Plants were then taken outside to be acclimatised. Seedlings were divided into two groups: control and treatment. Pots were colour coded with plastic tags. The flooding treatment was commenced by placing seedlings randomly inside three fibre-glass tanks filled with rain water (Figure 35). The water level was maintained at 15 to 20 mm above the soil surface. Control seedlings were kept on a table beside the tanks. During the experiment ambient temperature was recorded; the minimum temperature was 19°C and the maximum temperature was 34°C.

Figure 35: Waterlogging experiment involving three *Eucalyptus* species. Control plants in the foreground and treated plants in the background. Waterlogged plants were covered with wire mesh to reduce damage from birds. (14 March 1998).

Gas exchange measurements were made at irregular intervals, commencing from two weeks after the start of waterlogging. In addition, diurnal eco-physiological and environmental measurements were made on 10 April 1998. Gas exchange measurements (photosynthesis, transpiration, stomatal conductance and internal CO_2 concentration) were recorded for five samples of each of the three *Eucalyptus* species from both control and waterlogged treatment sets. Recordings were made every 3 hours between 0600 hours and 1800 hours local time using an open portable gas exchange system (LCA-3, Analytical Development Co., Hoddesdon, England) attached to a Parkinson leaf chamber (PLC-301 (3B). Photosynthetically active radiation (PAR), chamber temperature and ambient humidity were recorded before each reading. Other details are as in Chapter 3. Diurnal leaf water potential (ψ) of excised leaves were determined using a pressure chamber (Scholander *et al.* 1965) at 3 hour intervals. Five samples (from control and treatment) of each of the three species were used. All the leaves used for the water potential study were kept in labelled bags and added to respective seedlings at the end of the experiment for dry weight measurements.

All plants were harvested on 11 April. 1998, 65 days after the waterlogging treatment commenced. Each plant was carefully removed from its pot, washed, surface dried between paper towels, and placed in separately labelled bags. At this time observations were made of any morphological adaptations to waterlogging: roots, shoots, leaf colour (Royal Horticulture Society Colour Chart) and soil surrounding root parts. Samples were stored at 6°C and the following day, projected leaf area, length and width were determined using a digital image analyser (DIAS, Delta - T Devices, Cambridge, UK). Plants were then oven-dried at 105°C for 24 hours. Dry weights were obtained separately for shoots and roots.

Statistical analyses

Data were analysed using the Super ANOVA software program (Abacus Concepts, Berkley, Califonia) for one-way ANOVA. Residual plots of each ANOVA were obtained to examine homogeneity of variance. Based on residual plots, data were transformed to log or square root as appropriate and reanalysed. The data presented here are of uniformed means.

Results

No plants died during the experiment. Over the period of the experiment, increase in height of all three *Eucalyptus* species subject to waterlogging was consistently slower than the controls (Table 15). Height growth of *E. victrix* was least affected by waterlogging and no significant differences were observed in either *E. victrix* or *E. leucophloia.* Height growth was severely affected in *E. terminalis,* particularly towards the end of the experiment.

Table 15: Effect of waterlogging for 65 days on *E. victrix*, *E. terminalis* and *E. leucophloia*. Data are mean (± SD) of ten tallest seedlings (n= 10) from each species for height, number of leaves and leaf area, leaf length, width and length:width ratio.

	E. victrix			*E. terminalis*			*E. leucophloia*		
	Flooded (n=10)	Control (n=10)	*P*	Flooded (n=10)	Control (n=10)	*P*	Flooded (n=10)	Control (n=10)	*P*
Height (cm)									
09 days	21.20 ± (4.27)	21.63 ± (3.29)	NS	20.86 ± (1.16)	22.99 ± (1.61)	**	19.66 ± (2.99)	18.39 ± (3.74)	NS
23 days	23.72 ± (4.78)	24.17 ± (3.17)	NS	21.93 ± (1.01)	24.50 ± (1.91)	**	19.86 ± (2.79)	18.95 ± (4.13)	NS
31 days	24.06 ± (5.27)	26.41 ± (3.03)	NS	20.57 ± (2.06)	24.55 ± (1.79)	**	20.00 ± (3.04)	19.57 ± (4.36)	NS
38 days	24.98 ± (5.69)	27.20± (3.31)	NS	21.03 ± (3.04)	24.84 ± (1.76)	**	20.05 ± (2.80)	20.05 ± (4.23)	NS
59 days	25.23 ± (5.68)	28.23 ± (2.95)	NS	21.14 ± (3.07)	25.64 ± (1.78)	***	20.13 ± (2.78)	21.42 ± (4.57)	NS
No of leaves									
09 days	17.30 ± (2.98)	17.30± (3.88)	NS	18.00 ± (3.62)	21.70± (3.77)	*	20.80 ± (3.04)	18.20± (4.36)	NS
23 days	17.88 ± (2.52)	19.20 ± (5.30)	NS	17.90 ± (4.14)	21.30 ± (4.54)	NS	20.70 ± (2.75)	21.80 ± (5.18)	NS
31 days	17.20 ± (2.93)	19.80 ± (5.26)	NS	15.50 ± (5.08)	21.40 ± (3.83)	**	18.20 ± (4.41)	21.90± (5.02)	NS
38 days	16.60 ± (1.64)	21.30 ± (6.39)	*	15.00 ± (5.53)	22.60 ± (3.97)	**	17.20 ± (3.15)	23.30 ± (5.73)	**
59 days	15.50 ± (1.64)	20.30 ± (5.75)	*	14.00 ± (4.89)	21.90 ± (4.72)	**	13.20 ± (2.65)	23.30 ± (5.10)	***
65 days	14.50 ± (3.03)	19.10± (5.28)	*	12.90 ± (4.62)	21.60 ± (6.44)	**	10.50 ± (2.63)	23.60 ± (5.76)	***
Leaf area parameters									
Area (mm2)	110. 52 ± (19.57)	121.30 ± (10.3)	*	84.03 ± (21.75)	102.58 ± (10.47)	*	113.44 ± (22.51)	138.10 ± (38.46)	NS
Length (mm)	34. 77 ± (5.77)	38. 64 ± (3.84)	*	34.02 ± (25.56)	33.59 ± (5.69)	NS	24.68 ± (4.67)	33.54 ± 4.00	***
Width (mm)	16. 24 ± (2.22)	17. 37 ± (1.68)	NS	12.65 ± (3.36)	17.24 ± (1.94)	**	20.06 ± (3.42)	25.99 ± (3.61)	**
L: W ratio	2.15 ± (0.34)	2.23 ± (0.15)	NS	2.59 ± 1.49	1.95 ± (0.30)	NS	1.23 ± (0.06)	1.29 ± (0.05)	*

NS- indicates means are not significantly different. Significant differences: at $P < 0.05$*; $P <0.01$**; $P< 0.001$***.

Table 16: Mean (± SD) of shoot dry weight, root dry weight, whole plant and shoot/root ratio of tallest seedlings from each of *E. victrix*, *E. terminalis*, and *E. leucophloia* seedlings after 65 days of waterlogging.

	E. victrix			*E. terminalis*			*E. leucophloia*		
Attribute	Flooded (n= 10)	Control (n= 10)	*P*	Flooded (n= 10)	Control (n= 10)	*P*	Flooded (n= 10)	Control (n= 10)	*P*
Shoot dry wt(g)	2.66 ± (0.64)	3.33± (0.54)	*	1.51 ± (0.63)	3.05 ± (0.84)	***	2.55 ± (1.03)	4.18 ± (1.66)	*
Root dry wt(g)	0.64 ± (0.22)	3.54 ± (1.29)	***	0.37 ± (0.13)	2.92 ± (1.10)	***	0.53 ± (0.24)	2.22 ± (0.88)	***
Whole plant dry wt(g)	3.30 ± (0.73)	6.87 ± (1.33)	***	1.88 ± (0.69)	5.98 ± (1.33)	***	3.08 ± (1.18)	6.41 ± (2.46)	**
Shoot: Root ratio	4.77 ± (2.31)	1.05 ± (0.41)	***	4.37 ± (1.84)	1.23 ± (0.66)	***	5.66 ± (3.05)	1.94 ± (0.50)	**

Significant difference are $P < 0.05$*; $P < 0.01$**; $P<0.001$***. NS indicates means are not significantly different.

The number of leaves attached to the stem decreased within two weeks from initiation of waterlogging, particularly so in *E. terminalis* (Table 15). At this stage, *E. leucophloia* and *E. victrix* showed symptoms of leaf epinasty in flooded seedlings. Leaf number increased in *E. victrix* for the first 23 days after flooding. This was followed by a gradual decline. Flooding effects were almost similar towards the end of the experiment in both *E. terminalis* and *E. leucophloia* where both species had reduced numbers of leaves attached to stems. Flooding resulted in all three species producing significantly fewer leaves than the control from 38 days on.

At the end of the experiment (11 April 1998, 65 days after flooding) a substantial number of adventitious roots (mean 3.60 SD ± 1.44) was found only on waterlogged *E. victrix* with none on either *E. leucophloia* or *E. terminalis*.

At harvest (11 April 1998), roots of all seedlings showed considerable variation. Shoot dry mass, leaf number and leaf area differed in all three species. Differences in shoot dry mass due to flooding were significant in *E. victrix* ($P = 0.05$), *E. leucophloia* ($P = 0.05$) and *E. terminalis*. ($P = 0.001$) (Table 16). The effect was most pronounced in *E. terminalis*. Analysis of whole plant dry mass revealed significant differences in all three species. The effect was more severe in *E. vitrix* and *E. terminalis*. Analysis of shoot: root ratio showed differences in all three species.

Nine days after flooding there was no significant difference in transpiration rates of flooded and unflooded seedlings of *E. victrix* and *E. leucophloia*. However flooded *E. terminalis* seedlings had significantly lower transpiration rates than the control plants 9 days after treatment (Figure 36). However, after 23 days transpiration was significantly lower in flooded plants. Transpiration subsequently reduced in flooded *E. terminalis* and *E. leucophloia* but remained steady in *E. victrix*.

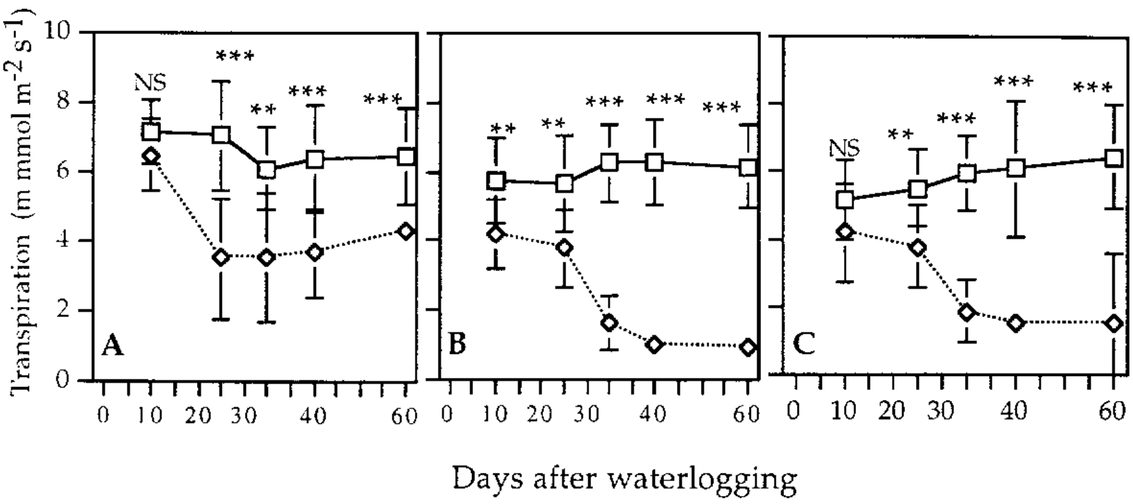


Figure 36: Changes in transpiration of *E. victrix* (A); *E. terminalis* (B) and *E. leucophloia* (C) of flooded (diamonds) and control (squares) seedlings. The first measurements were taken 9 days after exposure to flooding. Vertical bars indicate standard deviation of means of five measurements. NS indicates no significant difference; * indicates samples are significantly different: $^{**}P < 0.01$, $^{***}P < 0.001$.

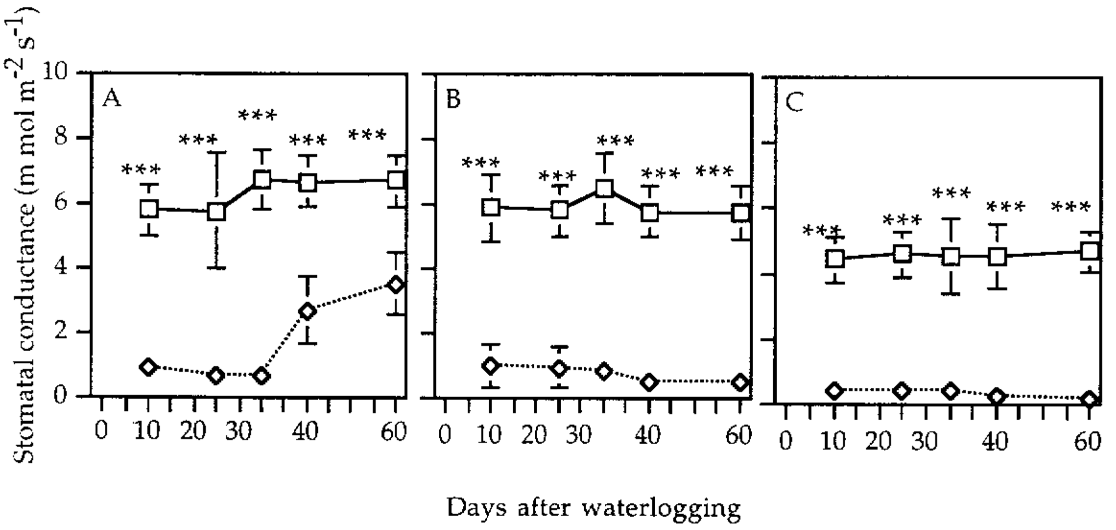


Figure 37: Stomatal conductance of *E. victrix* (A); *E. terminalis* (B) and *E. leucophloia* (C) of flooded (diamonds) and control (squares) seedlings. The first measurements were taken 9 days after exposure to flooding. Vertical bars indicate standard deviation of means of five measurements. * indicates samples are significantly different: $^{***}P < 0.001$.

Stomatal conductance was significantly different between flooded and control plants after 9 days of flooding (Figure 37) with rates between 4.2 and 6.8 mmol m^{-2} s^{-1} in unflooded plants. The range was only 0.3 to 1.1 m mol m^{-2} s^{-1} in all three species for flooded plants. Stomatal conductance remained low in flooded *E. terminalis* and *E. leucophloia* but in contrast stomata started to reopen in *E. victrix* 40 days after flooding, improving further by 60 days.

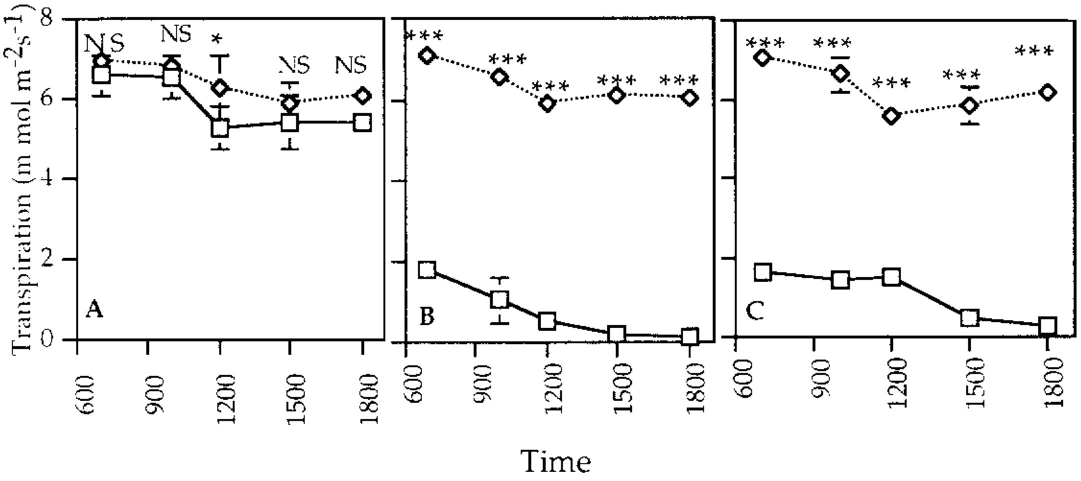


Figure 38: Diurnal patterns of transpiration of flooded (diamonds) and control (squares) seedlings of *E. victrix* (A); *E. terminalis* (B) & *E. leucophloia* (C) after 65 days of flooding. Values are mean (± SD) five. NS = no significant difference; * indicates samples are significantly different: **$P < 0.001$.

Diurnal transpiration of flooded *E. leucophloia* and *E. terminalis* plants was significantly lower ($P = 0.001$) than in unflooded seedlings. In *E. victrix* a marginally significant difference ($P = 0.043$) was observed at 1200 hr. The difference in transpiration rate of flooded and control *E. leucophloia* and *E. terminalis* varied from 5 - 7 m mol m^{-2} s^{-1} at each sampling time (Figure 38).

Except in *E. victrix* the diurnal stomatal conductance of control plants (Figure 39) exceeded 1.5 m mol m^{-2} s^{-1} and that of water-logged seedlings was between 1.0 and 1.5 m mol m-^{2} s^{-1} during the early part of the day. In both water-logged and control plants stomatal conductance declined progressively soon after sunrise. However, rates started recovering from 1500 hr.

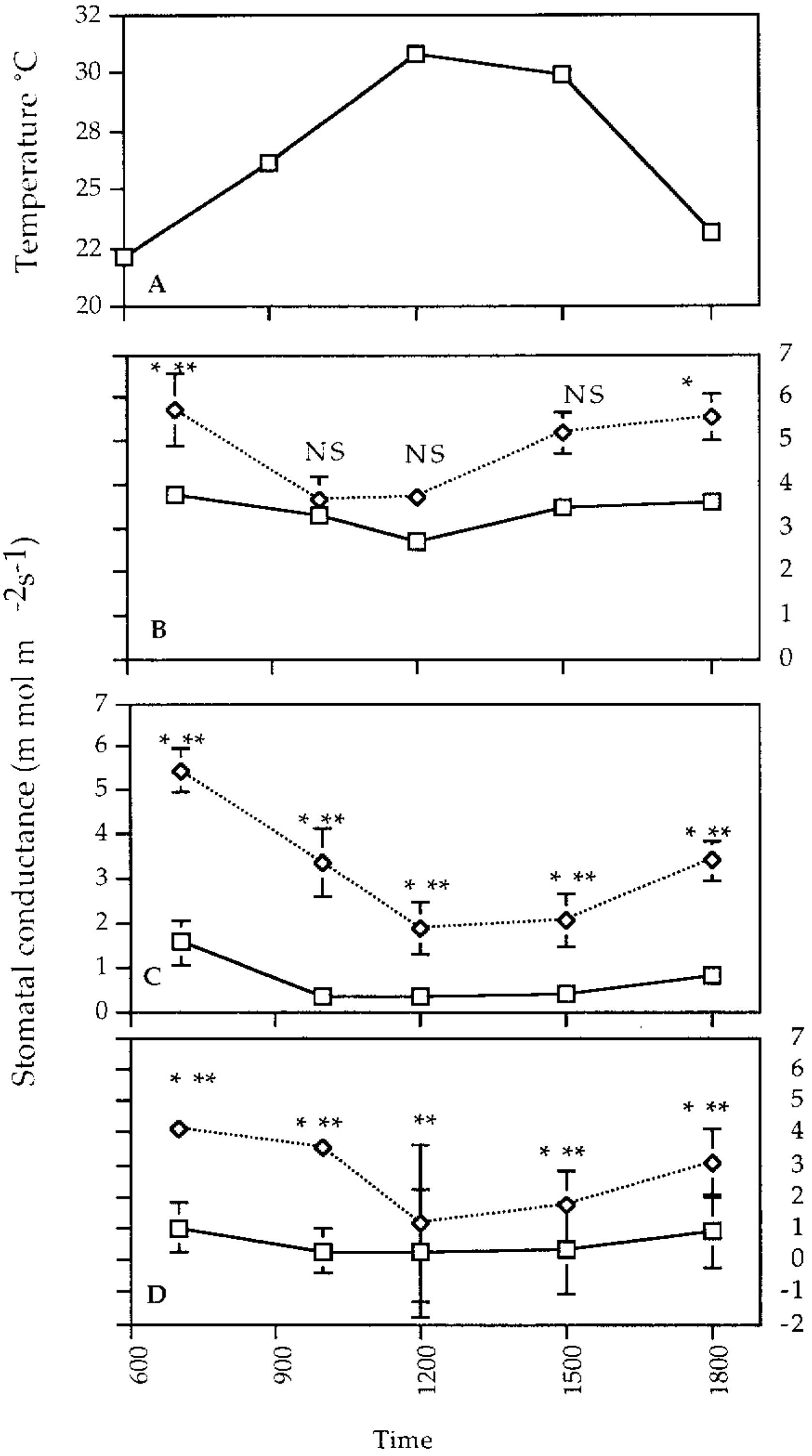


Figure 39: Diurnal patterns of stomatal conductance of flooded (squares) and control (diamonds) seedlings of *E. victrix* (B) ; *E. terminalis* (C) and *E. leucophloia* (D) after 65 days of flooding. Values are mean (± SD) for (n= 5) seedlings. NS indicates no significant difference, * indicate samples are significantly different $^*P < 0.05$; $^{**}P < 0.01$ & $^{***}P < 0.001$. (A) Temperature °C at the time of measurements.

Although diurnal mean leaf water potential (ψ) of waterlogged seedlings was consistently more negative than that of control plants, differences were only significant in *E. leucopholia* at 0600 hr (P = 0.026) and *E. terminalis* (P = 0.002) at 1200 hrs (Figure 40).

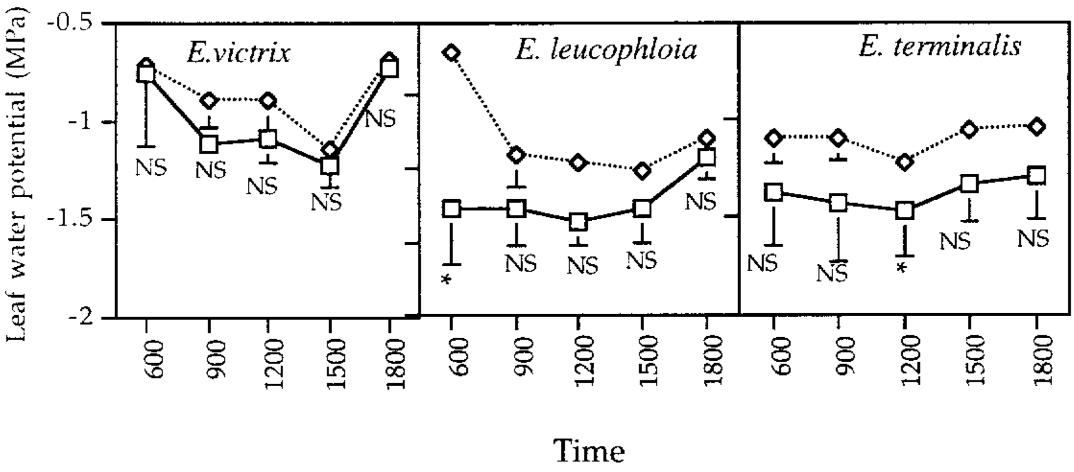


Figure 40: Mean pre-dawn leaf water potential patterns of flooded (squares) and control (diamonds) seedlings of *E. victrix* ; *E. leucophloia* and *E. terminalis* after 65 days of flooding. Values are mean (± SD) for (n= 5) seedlings and NS indicates no significant difference * indicate samples are significantly different *P < 0.05.

Within three weeks of waterlogging being imposed, leaf epinastic curvature was observed in waterlogged plants of *E. leucophloia* and *E. terminalis* but not in *E. victrix*. However, towards the end of the experiment this response had been observed in three plants of *E. victrix*. Between five and six weeks from waterlogging a mean of 4 to 5 leaves of *E. terminalis* and *E. leucophloia* had turned a yellow green colour (RHS Yellow Green Group C). Towards the end of the experiment these leaves became bright yellow (RHS Yellow Group B). Many were dead and fell off the stem before harvesting. Most young leaves of water-logged *E. victrix* seedlings were red purple in colour (RHS Red Purple group A). In contrast, most of the newly flushed leaves from control seedlings were red (RHS Red Purple group A). Control plants had formed two to three small branches from the main stem but no branches were produced on waterlogged seedlings in all three *Eucalyptus* species.

Stem hypertrophy was observed only in waterlogged *E. victrix*. Three weeks after waterlogging, adventitious roots had also formed on the submerged portion of most *E. victrix* stems and these floated just below the water surface. In contrast, neither *E. leucophloia* or *E. terminalis* waterlogged plants produced any adventitious roots. In most waterlogged plants, roots surrounded by soil had turned black. Most *E. victrix* water-logged plant roots were decayed, with some remaining old roots being soft and presumed dead. During the harvest (65 days after flooding), *E. terminalis* and *E. leucophloia* water-logged plant roots were black.

Discussion

The genus *Eucalyptus* has adapted to different ranges of climatic and edaphic factors. Whereas no species grows in a permanently waterlogged condition, a few species are able to grow in soil with some degree of waterlogging (Ladiges and Kelso 1977). The present study confirms the importance of adventitious root formation (at least in small plants) in *E. victrix* as an adaptation to withstanding waterlogging. A previous experiment with waterlogging of different-aged *E. victrix* seedlings revealed this adaptation to waterlogging (Chapter 3). In addition, stem hypertrophy may also be considered an important adaptation in *E. victrix*. Neither *E. terminalis* nor *E. leucophloia* produced any adventitious roots or showed stem hypertrophy when waterlogged. These species are presumed to be intolerant of waterlogging, as flood intolerant species seldom show any morphological changes and no recovery of gas exchange during the period of waterlogging (Tang and Kozlowski 1982).

Stem hypertrophy on the submerged portions of stems of *E. victrix* may assist with excretion of accumulated toxic compounds from the system (Gomes and Kozlowski 1986b). Production of adventitious roots may compensate for the death of older roots (Gomes and Kozlowski 1980a, Tsukahara and Kozlowski 1985).

Although no deaths occurred, water-logging of *E. terminalis* and *E. leucophloia* reduced dry mass of both above and below ground material. In both species, tips of lateral and tap roots had become very soft and some were visibly decaying. In addition, progressive decolouration was observed in a considerable number of leaves. It is emphasised that visual effects of waterlogging on these two species only started to become evident after 8 - 9 weeks. The rank of most flood tolerant to least tolerant is *E. victrix* > *E. leucopholia* > *E. terminalis*.

Adaptation to flooding by *E. victrix* is a combination of both morphological changes/responses: such as formation of adventitious roots and stem hypertrophy; and physiological adjustments, such as early stomatal closure and reduced transpiration rate. Further research is needed to study the effects of longer-term waterlogging on *E. terminalis* and *E. leucopholia*. Their absence from the floodplain is partially explained by the extent of detrimental effects and poor recovery following a period of waterlogging.

CHAPTER 5

Is there an association between the coolibah tree, *E. victrix* and the grass *S. dielsii* ?

Introduction

Vegetation in semi-arid and arid zones is often subject to short periods of abundant moisture. Nutrients may become limiting to biological production when moisture availability is not limited (West and Skujins 1978). Vertical and horizontal distribution of soil nutrients is strongly linked to vegetation distribution, composition, and biomass (West and Klemmendson 1978). Woody tree species can influence density and growth capacity of understorey plant species (Foster *et al.* 1984), or composition beneath the tree canopy (Haworth and McPherson 1994).

Grass production can be greatly enhanced by removal of trees (West 1969), but there is also evidence that trees may have a beneficial effect on growth of grass and other shrubs (*e. g.* Bosch and van Wyk 1970). Some grasses grow exclusively in close association with tree canopy cover with markedly higher productivity compared to grass growing in open areas (Kennard and Walker 1973). In the northern Transvaal low veld this association is thought to be due to higher soil nutrient availability under trees (Bosch and van Wyk 1970). Physical and chemical soil properties vary from the bole of the tree outwards (*e. g.* Belsky *et al.* 1989, Weltzin and Coughenour 1990) and nutrient gradients associated with an individual tree may contribute to a zonal pattern of herbaceous vegetation (Arnold 1964, Belsky *et al.* 1989, McPherson *et al.* 1991).

According to Wong *et al.* (1985) many C4 grasses, particularly those in the genera *Panicum* L. and *Setaria* L. grow well under wooded pasture conditions. Specific associations of the grass *Panicum maximum* Jacq., occur in Zimbabwe under the canopy of *Brachystegia spiciformis* Benth. and *Julbernardia* *globiflora* Benth. (Kennard and Walker 1973) and under large isolated specimens of *Acacia tortilis* (Forsk.) Hayne and *Adansonia digitata* L. in Kenya (Belsky *et al.* 1989).

The coolibah tree *E. victrix* has a widespread but scattered distribution across the central part of northern Western Australia including the Pilbara district (Brooker and Kleinig 1994). It is often abundant on seasonal flood plains and creek sides forming grassy, open woodlands that it dominates. It occurs where the land surface is weakly gilgaied. In coolibah woodlands of the Fortescue River floodplain north of Newman (lat. 23° 21'S, long. 119° 44'E) the vigorous annual grass species *Setaria dielsii* readily establishes and forms stands with clumps to 1 m high, beneath the canopy of mature *E. victrix.* This grass seldom occurs in open areas or under other tree or shrub species found in the coolibah woodland.

The aim of this study was to explore aspects of the joint occurrence of *E. victrix* and *S. dielsii.* In particular, whether soil nutrient status, moisture temperature or light help to explain the association.

Hypothesis

Growth and establishment of *S. dielsii* grass is not dependent on higher nutrient content, amount of light penetration through canopy and soil moisture, near the bole of *E. victrix* tree.

Methods

Soil sample

In February 1996, two soil samples of approximately 1 kg were taken for chemical analyses from 5-10 cm below the soil surface near each of ten randomly chosen *E. victrix* trees. One sample was taken from close to the main stem of each tree and a second sample was taken at a distance of 5 m from the bole. *S. dielsii* was present under five of these trees.

Soil nutrient analyses

Conventional methods were used for the chemical analyses. Available P and K were measured using the Colwell method. Nitrogen as NH_4^+ and NO_3^- was measured simultaneously using a Lachet Flow Injection analyser (Searle 1984). Combination electrodes were used to determine pH (both water extract and $CaCl_2$) and electrical conductivity calibrated against 0.01 m KCl. Organic carbon was obtained by the Walkley - Black (1934) method and sulphur by the KCl - 40 method (Blair *et al.* 1991). Iron was determined using a flame atomic absorption spectrophotometer at 248.3 nm.

Soil moisture

Using similar sampling methods three samples were taken for soil moisture analysis at each of 1, 3 and 5 m from the boles of the ten trees. These samples were placed in carefully sealed labelled tins. Initial masses were obtained using an electronic balance. Tins were then opened, placed in an oven for 24 hours at 105°C and re-weighed. Further soil moisture samples were taken from positions close to the bole, under the middle of the canopy and away from the canopy in May 1996 (20 trees) and March 1997 (5 trees, see below).

Soil temperature measurement

On February 16 and July 19, 1996, temperature probes were carefully buried in soil at 0 (surface), 10, 15 and 30 cm depths under the canopy of a representative *E. victrix* and in an adjacent open area. Air temperatures were also recorded 25 cm above the ground level. Probes were connected by wire cable to a data logger (Datataker DT 2000) connected to a battery and set to record at 10 min. intervals for 24 hr. A diskette (MF31M1-LCDAT01 / MELCARD Mitsubishi) was affixed to the data logger and data were down loaded to a Toshiba laptop computer. All temperatures were measured at mid-day and mid-night.

Above ground biomass

On March 24, 1997 above-ground biomass of herbage was taken from beneath five isolated *E. victrix* trees (as used for soil moisture). Quadrats of 1 x 1 m were placed adjacent to the bole, bellow the middle of the crown canopy and just beyond the canopy, along the four cardinal directions (n= 12 per tree). All herbage was clipped and bagged separately by species for each quadrat. This material was later dried at 105°C for 24 hr and dry weights obtained.

Light penetration through canopy and in open area.

On the same day a light meter (LI-COR, Inc, Model LI 185B/ QRPA 473-7808- Quantum Radio/ Photo meter), with hand held sensor, was used to quantify light penetration at each herbage quadrat site. Four readings, at cardinal corners, were taken for each (n= 48 per tree) between 11.30 and 12.30. Light penetration close to the bole and under the middle of the canopy was expressed as percentages of the mean readings taken beyond the canopy.

Statistical analyses

Means and standard deviations (standard errors for light penetration) were obtained and data sets contrasted using analysis of variance. Significance between means was tested using Fishers LSD test using Stat View 4.2.

Results

Soil analyses

Soil close to *E. victrix* where *S. dielsii* is present, is significantly higher in total N, Mg, K, S and electrical conductivity (EC) than at 5 m from the bole (Table 17). Soil samples do not differ significantly with respect to P, Ca, Na, organic C, Fe or pH although mean values of each of P, organic C and Fe are greatest near tree boles.

Table 17: Mean soil attributes (± SD) from close to the tree boles of *E. victrix* and 5 m away from the tree bole (n= 20).

Soil attribute	Position of samples		Significance	
	Under the trees #	5m away#	*P* =	+
Main nutrient elements				
Total N (mg/kg)	17.9 (± 10.1)	10.4 (± 2.99)	0.048	*
Available P (mg/kg)	37.5 (± 14.5)	29.70 (± 16.3)	0.270	NS
Available K (mg/kg)	1359 (± 127)	1090 (± 233)	0.007	**
Other macronutrients				
Extractable S (mg/kg)	7.97 (± 2.84)	4.29 (± 1.17)	0.004	**
Extractable Fe (mg/kg)	1012 (± 143)	941 (± 304)	0.510	NS
Exchangeable cations ^				
Ca (cmol(+)/kg)	13.26 (± 1.08)	13.63 (± 1.58)	0.550	NS
Mg (cmol(+)/kg)	4.14 (± 0.55)	3.64 (± 0.47)	0.043	*
Na (cmol(+)/kg)	0.12 (± 0.04)	0.12 (± 0.04)	1.000	NS
K (cmol(+)/kg)	4.14 (± 0.70)	2.94 (± 0.97)	0.006	**
Conductivity				
ECH_2O 1:5 (dS/m)	0.18 (± 0.05)	0.11 (± 0.02)	0.025	*
Organic carbon (%)	0.97 (± 0.50)	0.61 (± 0.33)	0.740	NS
pH H_2O 1:5	7.58 (± 1.58)	8.01 (± 0.15)	0.410	NS
pH 0.01M $CaCl_2$ 1:5	7.62 (± 0.08)	7.60 (± 0.12)	0.090	NS

n = 10 for each set; ^(cmol(+)/kg) = meq/100g; +*P* < 0.05 = * ; *P* < 0.01 = **; NS = not significant

Soil moisture

Although soil moisture is consistently higher closer to the tree bole than further away, this difference only reaches marginal significance on one occasion (Table 18).

Table 18: Soil moisture status (%) in relation to boles and crowns of *E. victrix* trees on three occasions. n = number of trees sampled, soil taken from 5 - 10 depth values with the same letter are not significantly different.

Date	Position in relation to tree						Statistics		
	Distance from bole								
	1 m		3 m		5 m		F =	*P* =	n
	Mean	SD	Mean	SD	Mean	SD			
February 1996	6.40	1.34	5.90	1.87	5.97	0.73	0.04	0.67	10
	Close to bole		Middle of canopy		Beyond canopy				
	Mean	SD	Mean	SD	Mean	SD			
May 1996	7.13 a	2.03	5.54 b	2.33	6.25 ab	2.36	2.52	0.09	20
March 1997	8.77	4.97	7.71	5.81	6.89	3.46	0.75	0.47	5

Soil temperature

During summer, soil temperatures at depth (10, 15 and 30 cm) are similar in the shade of *E. victrix* and beyond the canopy at midnight but differ during the day (Figure 41). Mid-night temperatures in both winter and summer are greatest at 30 cm. Shade temperature at 10 cm depth has a greater diurnal range in summer (12°C) than in the open (3°C). The reverse occurs in winter.

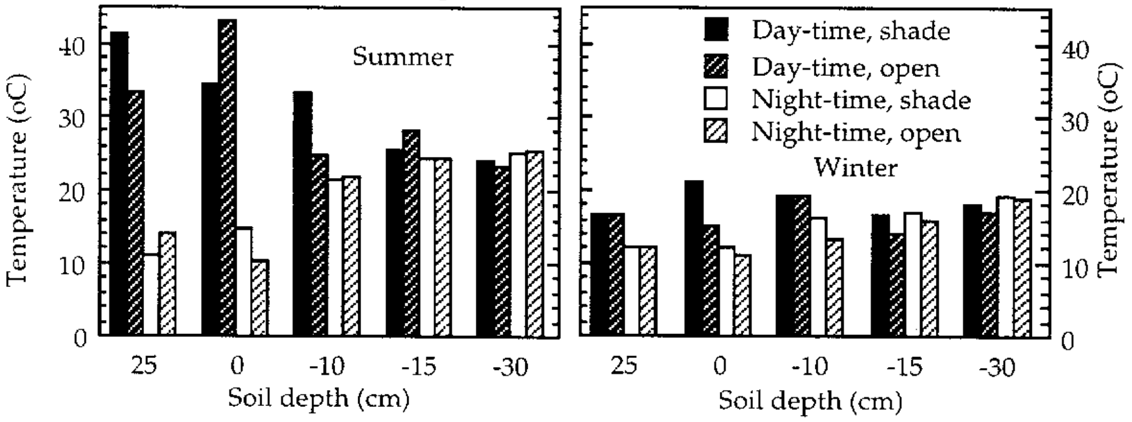


Figure 41: Temperatures at mid-day and mid-night at different positions in the shade of a *E. victrix* tree and nearby in the open. Readings taken on February 16-17 (summer) and July 19-20, 1996 (winter).

Summer surface soil temperature is lower in shade (34°C) at mid-day than the open (43°C) and 5°C warmer at night (15°C in shade vs 10°C in open). Summer diurnal ranges at the soil surface are 20°C under the canopy compared with 33°C in the open. Winter surface soil temperature is 6°C warmer under the canopy (21°C) at mid-day than in the open. At mid-night the winter surface temperature is 1°C warmer under the canopy than in the open.

Light penetration

Trees sampled in March 1997 are of mean height 5.93 m (SD ± 0.3); stem diameter, at 1.3 m, 38.9 cm (SD ± 6.1); and crown diameter 8.0 m (SD ± 1.5). Mean light penetration close to boles is 15 to 55% and at the middle of the canopy is 35 to 80% of that in the open (Figure 42). In each case, the position close to the bole is shadier than the mid-canopy position, but for two trees the difference is not significant. It is of interest that all five trees have a larger apparent crown spread in the N/S plane (9.0 ± 1.2 crown diameter) m than E/W (7.0 ± 1.0) m. This difference is significant (F= 61.85; $P = 0.0014$).

Significant differences occur between cardinal directions for light penetration (F= 16.29; $P = 0.0001$). Analysis of tree data sets indicates significant differences (3 of 5) for readings close to the bole and at the middle of the canopy for each tree (Table 19). Light readings suggest that trees 3, 4 and 5 cast most shade to the south of the bole whereas trees 1 and 2 have most shade to the west. Similarly, trees 1 and 4 are more open to the east, trees 3 and 5 to the west and tree 2 to the north.

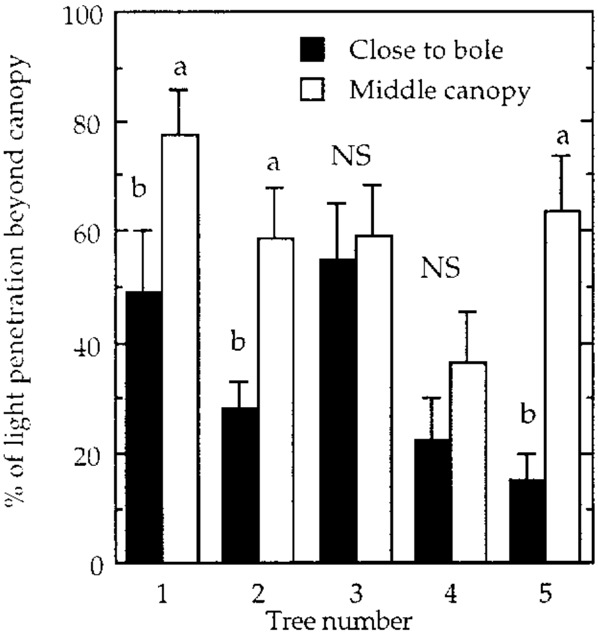


Figure 42: Light penetration at positions close to tree boles and under the middle of the canopy for five trees of *E. victrix*. Values are means of 16 readings and are expressed as percentages of light recorded beyond the canopy for each tree. Bars are standard errors of the means converted from interception values. Superscripts indicate significant differences ($P < 0.05$) between close to the bole and under the middle of the canopy by tree.

Biomass

Biomass sampled in association with *Eucalyptus victrix* at March 1997 includes seven perennial grass species and three annuals. Of these, *S. dielsii* has greatest biomass close to the bole and under the middle of the canopy (Table 20). Mean herbage biomass is greater under the tree canopy than beyond it, despite the latter being more diverse in species recorded.

Table 19: Mean light penetration at positions close to tree boles and at the middle of the canopy in the four cardinal directions, for 5 trees of *E. victrix*. Cell values are means of 4 readings, expressed as % of light recorded beyond the canopy for each tree. Analyses of variance made on actual values; dissimilar letters in rows indicate significant differences ($P = 0.05$) between cardinal directions.

Position	Tree No.	Cardinal direction				Statistics	
		North	South	East	West	F =	*P* =
Bole	1	73.8 a	15.8 b	96.1 a	9.3 b	11.585	0.001
Middle		99.6 a	77.8 a	96.8 a	36.6 b	7.564	0.004
Bole	2	33.2	42.3	14.7	22.4	1.512	0.262
Middle		99.3 a	32.2 b	78.3 a	24.1 b	14.791	<0.001
Bole	3	62.8	15.3	45.3	83.2	1.583	0.245
Middle		58.4 ab	30.7 b	52.6 ab	94.9 a	2.702	0.092
Bole	4	12.2 b	5.7 b	62.7 a	9.3 b	7.216	0.005
Middle		54.5 a	5.0 b	72.0 a	14.0 b	6.666	0.007
Bole	5	8.0 b	1.8 b	4.4 b	68.8 a	20.675	<0.001
Middle		90.6 a	2.9 b	69.5 a	90.6 a	17.931	<0.001

Table 20: Mean above ground biomass (g m^{-1}) of species at the centre (bole), middle and beyond the canopy of *E. victrix* (n = 5, sampled at March 1997). P = perennial; A = annual; G = grass; H = herb; SS = sub-shrub; R = runner. Names after Green (1985).

SPECIES	Life form	Canopy position		
		Centre	Middle	Beyond
Astrebla pectinata (Lindley) F. Muell. ex Benth.	PG	0.30	-	-
Boerhavia paludosa (Domin) Muikle	AH	-	-	0.01
Cenchrus ciliaris L.	PG	0.11	3.07	0.15
Corchorus tridens L.	SS	-	0.19	0.43
Dactyloctenium radulans (R. Br.) P. Beauv.	AG	-	15.18	13.97
Dichanthium sericeum (R. Br.) A. Camus	PG	0.28	3.09	2.09
Eragrostis japonica (Thunb.) Trin.	AG	0.11	1.54	0.14
Eragrostis setifolia Nees	PG	0.68	10.28	32.42
Eriachne benthamii (Domin) Hartley	PG	-	3.02	2.53
Eriochloa pseudoacrotricha (Stapf ex Thell.) J. Black	PG	-	-	0.61
Euphorbia boophthona C. Gardner	AH	-	0.03	2.24
Evolvulus alsinoidies (L.) L.	PH	-	-	6.00
Malvastrum americanum (L.) Torrey	SS	91.14	44.33	1.57
Mukia maderaspatana (L.) M. Roemer	R	8.75	0.84	0.19
Neptunia dimorphantha Domin	PH	0.01	-	-
Operculina aequisepala (Domin) R. W. Johnson	R	5.74	5.45	6.49
Panicum decompositum R. Br.	PG	0.64	3.29	0.88
Rhynchosia minima (L.) DC.	R	0.01	0.28	-
Rostellularia pogonanthera F. Muell.	AH	-	10.92	2.76
Salsola kali L.	AH	-	3.41	0.93
Setaria dielsii Herrm. in Rosen	AG	37.58	33.87	4.42
Triraphis mollis R. Br.	PG	-	1.26	1.61

The introduced sub-shrub *Malvastrum americanum* exceeds *S. dielsii* in mean biomass at both canopy positions and occupies 80% of sampled quadrats close to tree boles. The grass has more occupied quadrats than *M. americanum* at the middle of the canopy position. These two species constitute the bulk of material found under the *E. victrix* trees sampled. Other grasses become more abundant away from the trees. Elsewhere in the floodplain the perennial grass *Panicum decompositum* is often more abundant.

New foliage of this species is highly palatable to cattle and is also taken by locusts in season.

Comparison of mean biomass by position and cardinal direction indicates significantly greater values to the north for *M. americanum* (Table 21). However, this species is more frequent in quadrats south of the trees. Biomass of *S. dielsii* is greatest to the east at positions close to the bole, and to the west at the middle of the canopy. These differences are not significant.

Table 21: Biomass (g m^{-1}) representation by cardinal direction and canopy position of *M. americanum* and *S. dielsii* in relation to five trees of *E. victrix* at March 1997. Numbers in brackets are quadrats occupied by the species. (Maximum per entry = 5)

Position Species	Quadrats	Cardinal direction				Statistics		
		North	South	East	West	F =	*P* =	n =
Bole								
M. americanum	All	139.5(3)	69.0 (5)	74.7 (4)	81.4 (4)	0.654	0.592	20
	Occupied	232.4 a	69.0 b	93.3 b	101.8 b	4.361	0.027	16
S. dielsii	All	16.0 (2)	31.7 (2)	74.6 (4)	27.4 (5)	1.356	0.292	20
	Occupied	40.1	79.3	93.3	27.4	1.501	0.279	13
Middle								
M. americanum	All	42.9 (1)	45.4 (3)	74.7 (2)	27.4 (3)	0.505	0.684	20
	Occupied	214.6 a	75.7 b	186.7 a	24.5 b	8.954	0.019	9
S. dielsii	All	21.8 (5)	48.4 (3)	6.0 (1)	59.3 (3)	0.938	0.446	20
	Occupied	21.8	80.7	30.1	98.8	1.217	0.364	12
Beyond								
M. americanum	All	6.0 (1)	0	0	0	-	-	20
	Occupied	31.4 (1)	-	-	-	-	-	1
S. dielsii	All	0.6 (1)	0.5 (1)	8.9 (2)	7.7 (1)	0.715	0.557	20
	Occupied	3.0	2.7	22.2	38.3	0.654	0.696	5

Discussion

Accumulation of litter may affect the chemical composition of soil beneath long-lived individual plants of arid and semi-arid areas (Roberts 1950, Fireman and Hayward 1952, Paulsen 1953). Both soil moisture and soil temperature can be influenced by the tree canopy. The canopy can reduce evaporation and thereby enhance soil moisture (Weltzin and Coughenour 1990) and reduce soil temperature near the tree bole (Tidemann and Klemmedson 1977).

Slightly higher soil moisture close to boles may be partly due to stemflow (Callaway *et al.* 1991). This is unlikely to be a major source with *E. victrix* as most moisture in the longer term may come from flooding. This is likely to equalise soil moisture among and under trees, apart from those on raised mounds that are a feature elsewhere in the Fortescue River floodplain. Trees of *E. victrix* tend to have long, near surface roots that spread beyond the canopy, probably contributing to soil drying beyond the crown spread. The question of enhanced growth of *S. dielsii* being associated with moisture levels requires further examination.

Concentration of the grass *S. dielsii* under *E. victrix* trees coincides with higher soil nutrient levels close to the tree boles. Higher levels of nitrogen and potassium in particular may benefit this grass; sulphur and magnesium perhaps less so. Belsky *et al.* (1989) found significantly greater grass production under tree canopies to be particularly associated with higher nitrogen levels. As minerals are not absorbed in proportion to their abundance in substrates, variations in soil chemistry will occur under different species dependant on their litter chemistry (Charley and West 1975). Deciduous trees have regular massive litterfalls that can contribute to nutrient enrichment and gradients around trees (Callaway *et al.* 1991). The evergreen nature of *E. victrix*, coupled with its rather thick and slow to decay foliage, implies that redistribution may be less dramatic. Gutierrez *et al.* (1993) reported significantly higher soil nitrogen, phosphorus and organic matter beneath the canopy of *Porliria chilensis* shrubs (Zygophyllaceae) and Tiedemann and Klemmedson (1973) find more nitrogen, potassium, sulphur, soluble salts and organic matter in soil under mesquite trees than between trees. In the northern Transvaal the *Panicum* - tree association is thought to be mainly due to soil enrichment by the tree (Bosch and Van Wyk, 1970).

Trees enhance soil fertility through litterfall. Organic matter may provide much of the exchange capacity of surface soil as well as improving soil structure (Campbell *et al.* 1993). Large trees of *E. victrix* accumulate much exfoliated bark and fine branchwood beneath their canopies as well as insect detritus. In addition, branch holes in the trees are favoured nesting sites for the budgerigar (*Melopsittacus undulatus*) and faunal contributions to nutrient enhancement may be significant (Belsky *et al.* 1989). It is most likely then that, in common with other tropical tree species, the enhanced nutrient status associated with *E. victrix* trees appear to contribute to the relative abundance of *S. dielsii* in association with this tree.

An indication of the role of light is provided in that *S. dielsii* biomass close to boles appears greater to the east side (at least for those trees examined) where more light is available at ~ 45% of full sunlight. It is observed that this grass has the capacity of branching continuously as it grows upwards and that the plants may lean away from tree boles, particularly to the east. In contrast, beneath the middle of tree canopies greatest *S. dielsii* biomass occurs to the south and west. Light penetration here averages 30-45% of full sunlight. The sub-shrub *M. americanum* may competitively inhibit *S. dielsii* near tree boles at lower light intensities. Under the canopy there is an inverse relationship between the two species at light penetration greater than 50%.

Increased herb layer productivity under canopies is associated with both enhanced soil fertility and lower soil temperatures (Belsky *et al.* 1989). Possibly the scarcity of *S. dielsii* in more open areas may be related to higher soil temperatures and greater fluctuations in temperature. Temperature fluctuations at the soil surface may both condition seed and provide a suitable germination environment for *S. dielsii* (Lunt 1995). High temperatures also reduce the growth of some forbs (Willis and Groves 1991) and persistence of the competitive *M. americanum* is clearly linked to either shade or a correlative environmental factor. Decreased density of *S. dielsii* towards the edge of the canopy is probably due to a combination of factors, including competition for light (Parker and Muller 1982), and soil moisture (Tiedemann and Klemmedson 1977, Smith and Stubbendieck 1990) or to competition from other species (Schott and Pieper 1985).

Relative scarcity of native perennial grasses under *E. victrix* may partly result from prior cattle grazing pressure. *S. dielsii* is a rapid-growing annual that may temporarily smother and outcompete seedling growth of slower growing perennial grasses. The presence of perennial grasses at favourable sites is more likely in natural, ungrazed systems (Moyo and Campbell 1996). *M. americanum* is not taken by cattle. This species may protect *S. dielsii*, once established, from grazing pressure. When this annual grass has died away from mid-year the more palatable perennial grass species may lack sufficient vigour to re-occupy the site unless extensive flooding has intervened.

CHAPTER 6

Competition between seedling *E. victrix* and grass species

Introduction

During the growth phase of a particular plant, competition for resources is not between all plants of the population, but only between those individuals immediately surrounding it (Harper 1977, Antonovics and Levin 1980). Competition between or within plant species can be demonstrated in two ways: by field experiments to explain the spacing patterns; and by pot trial experiments that minimise variation in all other factors that affect growth.

Competition in plant communities implies that the supply of light, water or nutrients to plants is reduced by the presence of their neighbours and their proximity to either the same or different species (Harper 1977, Tilman 1982). The competition effect and intensity is dependent on the number of neighbours. When plant density is high individual plants can interfere with each other, in activity above and below the soil surface and may also change the environment (Mack and Harper 1977).

Plant competition for available soil moisture is generally very high in arid and semi-arid environments (Anderson 1967). In addition to water, plants also compete for soil nutrients (Robberecht *et al.* 1983, Ehleringer 1984, Fisher *et al.* 1988). Studies on competition between grass and tree seedlings demonstrate that tree seedling survival depends on effectiveness of competition from grasses (Withers 1978, Noble 1984, Davidson and Reid 1985). Competition from grasses for moisture is a major cause of failure of *E. camaldulensis* seedlings to establish (Dexter *et al.* 1986). High mortality rates of blue oak seedlings are due to competition from annual grasses and forbs (Gorden *et al.* 1989). Danielsen and Halvorson (1991) found perennial grasses stunt growth of valley oak seedlings by utilising the soil moisture.

Competition occurs within woodlands between trees, shrubs and grasses that differ in rooting depth, leaf area and life cycle biomass (Walker *et al.* 1986). Seedlings of woody plant species do not compete well with grass species (Van Auken and Bush 1988, Bush and Van Auken 1990). *Pinus resinosa* (red pine) seedling shoot and root growth is suppressed by interference from three grass species *Agropyron repens* (L.) Beauv., *Agrostis alba* L. and *Poa palustris* L. (Caldwell *et al.* 1995). Within annual and perennial grasses, the annual grasses use soil moisture faster than perennials (Jackson and Roy 1986).

Three variables: germination date, density and pattern are important in competition. Different emergence times can greatly affect competitive ability. The first seedlings to emerge are likely to be highest in production simply because they can access resources and utilise most of the available resources (Ross and Harper 1972, Fowler 1986). Sakai (1957) shows density is a major factor contributing to reduction in above and below ground biomass.

Competition in a natural system may be inter-specific or intra-specific. Inter-specific competition is often more intense than intra-specific competition. In monoculture, intra-specific competition tends to a balanced relationship between the mean yield per plant and its density (Shinozaki and Kira 1956). In mixtures of two species, the mean yield of a species is dependent on the relative frequency of both species and also on overall density (Harper 1977).

Figure 43: *E. victrix* seedlings (marked with red flagging on wire stakes) surrounded by annual herbs, Marillana (Chapter 2). These seedlings germinated after good summer rain in early 1995. Photograph taken 3 May 1995. (**1**) *Psoralea cinerea* Lindley in Mitch. (**2**) *Ptilotus macrocephalus* (R. Br.) Poiret.

Coolibah woodland of the Fortescue floodplain contains areas of trees different sized (Chapter 2). This suggests that recruitment and renewal of *E. victrix* is episodic. Biological activity in the floodplain is greatest in the summer period when most moisture is available. Available evidence suggests that *E. victrix* germinates after good summer rainfall and/or flooding events and provided seed is in suitable places, seedlings may establish (Chapter 2). Large numbers of annual grasses also emerge in summer and extant perennial grass plants will green up provided they have not been inundated for too long. Annual herb growth is also partly stimulated by good moisture conditions early in the year (Figure 43) but other herbs, including a number of annual Asteraceae species, grow well with winter rain (May-July). By October / November in most years, the herbage dries off and most annuals are dead.

The period of persistence of newly produced *E. victrix* seedlings is variable (Chapter 2). It is dependent on availability of soil moisture which is affected by competition from neighbouring species. Competition may differ depending on size of competitors when the *E. victrix* seedlings commenced growth. Presumably, if *E. victrix* seed germinates among dense grass it may not have as great a chance of survival due to competition effects as it would with fewer, or no, other plants present. Possibly, *E. victrix* seedlings and grass species may exploit different rooting depths. As conditions become drier each year, competition for scarce soil moisture between newly recruited seedlings, already established grasses and mature *E. victrix* trees is likely to intensify. Few seedlings of *E. victrix* can persist over the period from September to the following summer rains (Chapter 2). An understanding of competition between *E. victrix* and grass species is fundamental to confirming the cycle of germination, seedling establishment and early mortality.

Seedling densities of *E. victrix* on a unit area basis are not high (Chapter 2). This suggests that either seedfall is rather limited or that intra-specific competition is high in this species.

This Chapter investigates inter-specific competition between *E. victrix* and three grass species at different densities (*S. dielsii* , *Cenchrus ciliaris* L., and *P. decompositum*) in controlled conditions by means of a pot trial experiment. A parallel set of treatments involving different densities (intra-specific competition) in *E. victrix* is also reported. The singleton treatment in this set is used as a control for the grass mixtures. All treatments were set out using three different pot sizes to test differences in available root space.

Grass selected for trial

C. ciliaris (buffel grass). This species is native to India and Southern Africa and is naturalised in semi-arid regions of Australia. It is a coarse, tufted, perennial grass with a height of 60 - 100 cm. The seed head is a bristled spike 5 - 15 cm, purple when young, becoming white at maturity. Leaf blades are flat, 5 - 10 mm wide and 8 - 30 cm long (Roberts and Silcock 1993). This is a common species in well watered areas but cannot withstand flooding.

S. dielsii (Diel's pigeon grass). An annual grass attaining heights of 1 m. The panicle is spike-like, 3 -12 cm long. Leaves are dark green. *S. dielsii* is found under the canopy zone of *E. victrix* trees in the study area (Chapter 5).

P. decompositum R. Br. (native millet). A butt-forming perennial grass, sometimes short lived. Attained heights are 45 to 105 cm. Leaves are bluish green, 10 - 25 cm long, flat, erect and tapering at the tip. At the base there is an accumulation of white papery dead leaves from the previous year. The inflorescence is a loose open panicle up to 40 cm long and almost as wide.

Null hypotheses

i) *E. victrix* seedling growth is not affected by grass density.

ii) There is no difference in *E. victrix* survival and growth between early and later grass establishment.

iii) Inter-specific competition is not more intense than intra-specific competition in *E. victrix*.

iv) Growth of *E. victrix* seedlings is not dependent on available growing space.

Materials and Methods

Inter-specific competition between *E. victrix* and grass species (mixed culture).

The three different grass species (one annual and two perennial) *S. dielsii*, *P. decompositum* and *C. ciliaris* chosen, all occur in the same environment. Three densities of grass: high, medium and low (Table 22) were represented by one, two or three individual plants respectively from each species with a single *E. victrix* seedling (Figure 44).

Three different sizes of pots were selected to provide variation in available growing space; small (140 mm), medium (200 mm), and large (250 mm in diameter). Plantings of *E. victrix* and the grasses plants were made on three different dates. The first date was on the "same day" when both *E. victrix* and the grass species were planted simultaneously on 08. 02. 1997. The second date was "late grass" where the *E. victrix* was again transplanted on 08. 02. 1997, followed by the grass on 22. 02. 1997. The third planting date was "early grass", in which the grass species were introduced to pots on 25. 01. 1997 and 14 days later *E. victrix* was planted (08. 02. 1997). The 14 day period between transplanting is based on the time taken for *E. victrix* to establish (Chapter 2).

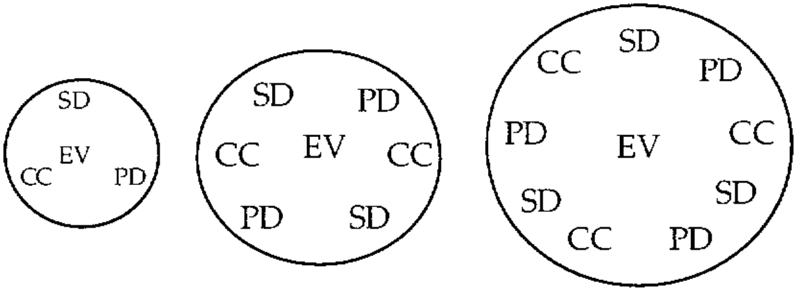


Figure 44: Diagrammatic representation showing positions of *E. victrix* (EV) and grass species *C. ciliaris* (CC), *S. dielsii* (SD) and *P. decompositum* (PD), planted at 1, 2 or 3 each per pot.

The *E. victrix* seedlings were planted in the centre of the pot. Grass species were planted peripherally, with species alternating (Figures 44 and 45). Treatments were arranged in a completely randomised design. Replicates were randomly located on a table in the glass house. Pots were rearranged randomly over the experimental period to allow all pots to receive the same amount of light.

Table 22: Experimental layout for the trial investigating competition effects of three species of grass on *E. victrix* (all *E. victrix* planted on 08.02. 1997).

Size of the pot (mm)	Time	Density of grass species			Total Density	Replicate (n)
		Pd	Sd	Cc	+ E. v	
Small (140)	Early Grass 25. 01. 1997	1	1	1	3 + 1	7
		2	2	2	6 + 1	7
		3	3	3	9 + 1	7
	Late Grass 22. 02. 1997	1	1	1	3 + 1	7
		2	2	2	6 + 1	7
		3	3	3	9 + 1	7
	Same day 08. 01. 1997	1	1	1	3 + 1	7
		2	2	2	6 + 1	7
		3	3	3	9 + 1	7
Medium (200)	Early Grass 25. 01. 1997	1	1	1	3 + 1	7
		2	2	2	6 + 1	7
		3	3	3	9 + 1	7
	Late Grass 22. 02. 1997	1	1	1	3 + 1	7
		2	2	2	6 + 1	7
		3	3	3	9 + 1	7
	Same day 08. 02. 1997	1	1	1	3 + 1	7
		2	2	2	6 + 1	7
		3	3	3	9 + 1	7
Large (250)	Early Grass 25. 01. 1997	1	1	1	3 + 1	5
		2	2	2	6 + 1	5
		3	3	3	9 + 1	5
	Late Grass 22. 02. 1997	1	1	1	3 + 1	5
		2	2	2	6 + 1	5
		3	3	3	9 + 1	5
	Same day 08. 02. 1997	1	1	1	3 + 1	5
		2	2	2	6 + 1	5
		3	3	3	9 + 1	5

Pd = *P. decompositum*, Sd = *S. dielsii*, Cc= *C. ciliaris* and Ev = *E. victrix*

Figure 45: 1] small, 2] medium & 3] large pots. (1) with low density [3 + 1]; (2) medium density [6 + 1] & (3) High density [9 + 1] of grass species and *E. victrix*. The photo was taken 21 days after treatment commenced (Early grass treatment).

Intra-specific competition of *E. victrix* seedlings (monoculture).

A monoculture of *E. victrix* was grown at the same time. Densities were 1, 4, 7 or 10 *E. victrix* seedlings per pot, all planted on 08. 02. 1997. Ten replicate pots of each density were used in small (140 mm) and medium pots (200 mm); five replicates of large pots (250 mm) were used. The set of one per pot is also used as a control for the inter-specific competition trial (Figure 46).

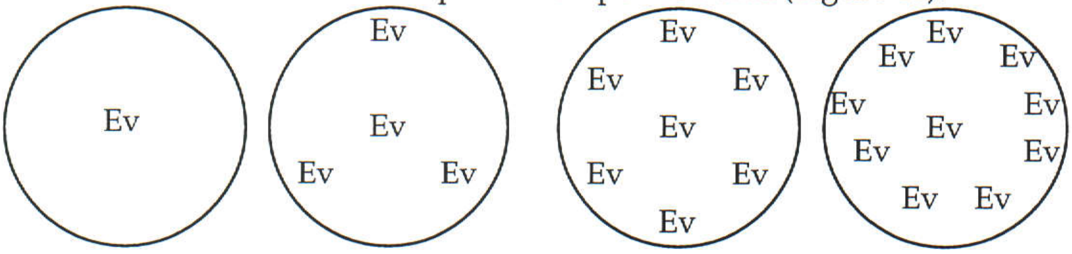


Figure 46: Diagrammatic representation of a monoculture of *E. victrix* (EV) pots.

General methods for both inter-specific and intra-specific trials.

Soil from 0-15 cm deep (surface litter removed), was collected from coolibah woodland in the Fortescue floodplain in February 1996. It was bagged and transported to Curtin University Field Trial Area. Prior to use it was passed through a wooden (48.5 cm in diameter, 2 mm mesh) sieve to remove any stones or dead plant material. It was then thoroughly mixed by turning in an electrically driven cement mixer for 20 min. before being placed in pots.

Seeds of *E. victrix* and *S. dielsii* were collected in April 1994 and those of *C. ciliaris* were collected 5 May 1995, from coolibah woodland at Ethel Creek. Seeds of *P. decompositum* were purchased (1996) from Nindethana Seed Ltd, WA. All seeds were stored in separately labelled jars in the laboratory at 21°C (room temperature) until used. Seed lots were set out on 10 and 18 of January 1997 in black, plastic seeding trays (35 x 29 x 5.5 cm) containing sterilised coarse sand and lined with paper towelling at the bottom of each tray. These trays were placed inside larger white butcher's trays of 43 x 30 x 6 cm. Water was added to the larger trays three times a week. The whole set up was placed on a heat bed (approximately 25°C). Transplanting commenced on 25. 01. 1995 for the early grass and finished on 22. 02. 1997 for the later grass. All other seedlings were planted on 08. 02. 1997. After transplanting pots were lightly watered with rain water and then placed in a glass house. Any dead seedlings were replaced two to three days from transplanting.

At transplanting, care was taken to allocate seedlings by size to the various treatments such that no treatment had disproportionately large or small seedlings of a species. After transplanting, pots were lightly moistened with rain water and then placed on benches in a glasshouse. Any deaths in the first three days were replaced. Initially, seedlings were moistened with rain water four times a week to the end of March and thereafter twice a week.

All plants were harvested after 63 days (12. 04. 1997). Plants were carefully removed by inverting pots and gently extracting contents onto a wire mesh table. Soil was washed away and intermingled roots of *E. victrix* carefully separated in water. Grass roots were left mixed and placed in separately labelled bags after mopping with paper towels.

E. victrix plants were separated into root and shoot portions and placed in separately labelled bags. Plants were initially stored at 5°C to allow determination of projected leaf area, length and width using a digital image analyser (DIAS, Delta-T Devices, Cambridge, UK). Shoot and root mass were then obtained after drying at 105°C for 24 hr.

Statistical analyses

Data were analysed using Super ANOVA and STATVIEW 4.2 (Abacus Concepts, Berkley, California). Minitab 8.2 was used for multivariate analysis. Residual plots of each ANOVA were obtained to examine homogeneity of variance. Data were then log or square root transformed as required and reanalysed. Means were compared using Tukey's HSD test (Day and Quinn 1989).

Results

Seedling survival

Mixed culture

When planted on the same day as the grass seedlings, *E. victrix* persisted for 4 weeks but mortalities were observed from 5-6 wk in the small pots. By completion of the trial (9 wk), no *E. victrix* seedlings had died in either of medium or large pots when established at the same time as the grass or before the grass. Some mortalities occurred in all pot sizes when grass was established before *E. victrix* at medium and high densities (Figure 47). When *E. victrix* was planted before the grasses the only deaths observed were in the high density small pots.

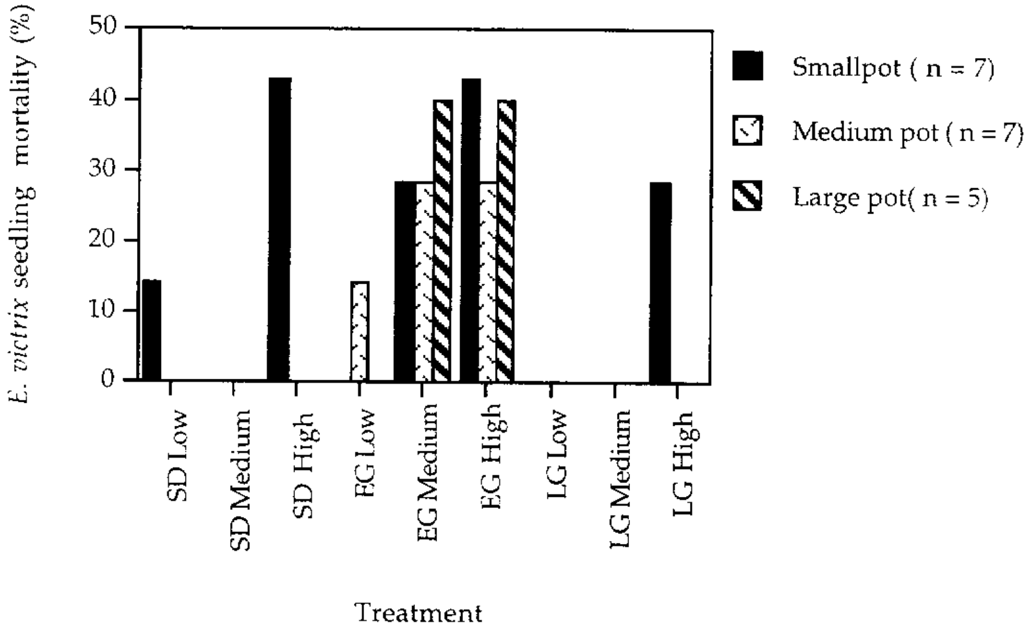


Figure 47: Percentage of mortality of *E. victrix* at (9 wk) grown in one of three pot sizes with grasses, where: SD = grass and *E. victrix* planted together; EG = grass planted first; LG = *E. victrix* planted first. Low, medium and high refer to grass densities of 3, 6 or 9 plants per pot respectively.

Monoculture

In the monoculture stand, *E. victrix* mortality was highest in the large sized pots, with losses at all densities more than 1 (Figure 48). Some losses also occurred in small and medium sized pots at medium and high densities.

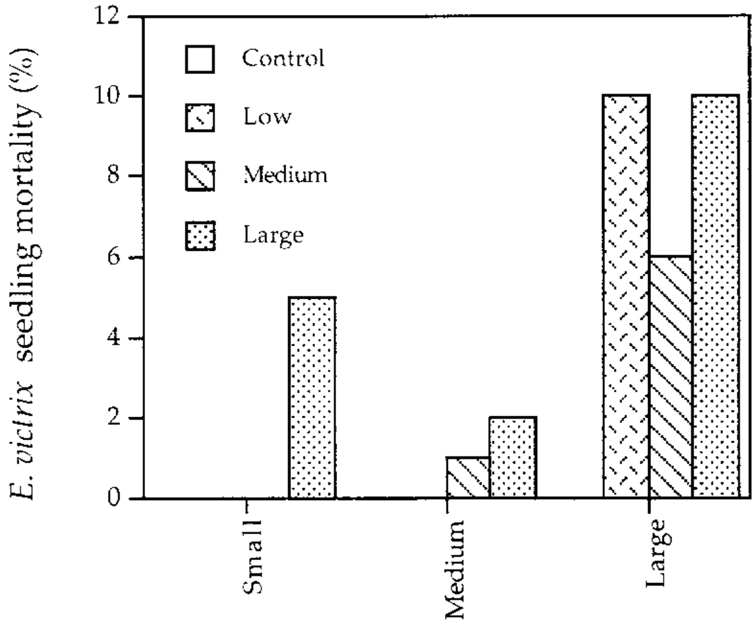


Figure 48: Percentage of mortality of *E. victrix* (at 9 wk), grown in one of three pot sizes in monoculture where control = 1; low = 4; medium = 7; and high = 10 *E. victrix* seedlings per pot respectively.

Table 23: Two-way analysis of variance for surviving seedlings for monocultured *E. victrix* seedlings.

Factor	df	MS	F value	*P* value
Density [D]	3	0.150	3.985	0.010^{**}
Pot size [P]	2	0.197	5.219	0.007^{**}
D x P	6	0.056	1.486	0.192^{NS}
Residual		0.038		

** $P < 0.01$. NS = Not significant.

The numbers of surviving seedlings from the monoculture treatment were analysed using a two-way analysis of variance. This reveals a significant difference in survival with density ($P = 0.0103$) and pot size, ($P = 0.0072$). but the interaction was not significant ($P = 0.1922$) (Table 23).

Growth Comparison

Monoculture

The *E. victrix* seedlings grown one per pot had grown significantly (P = 0.001) taller than those grown at > 1 per pot in all pot sizes (Figures 49, 50, and 51).

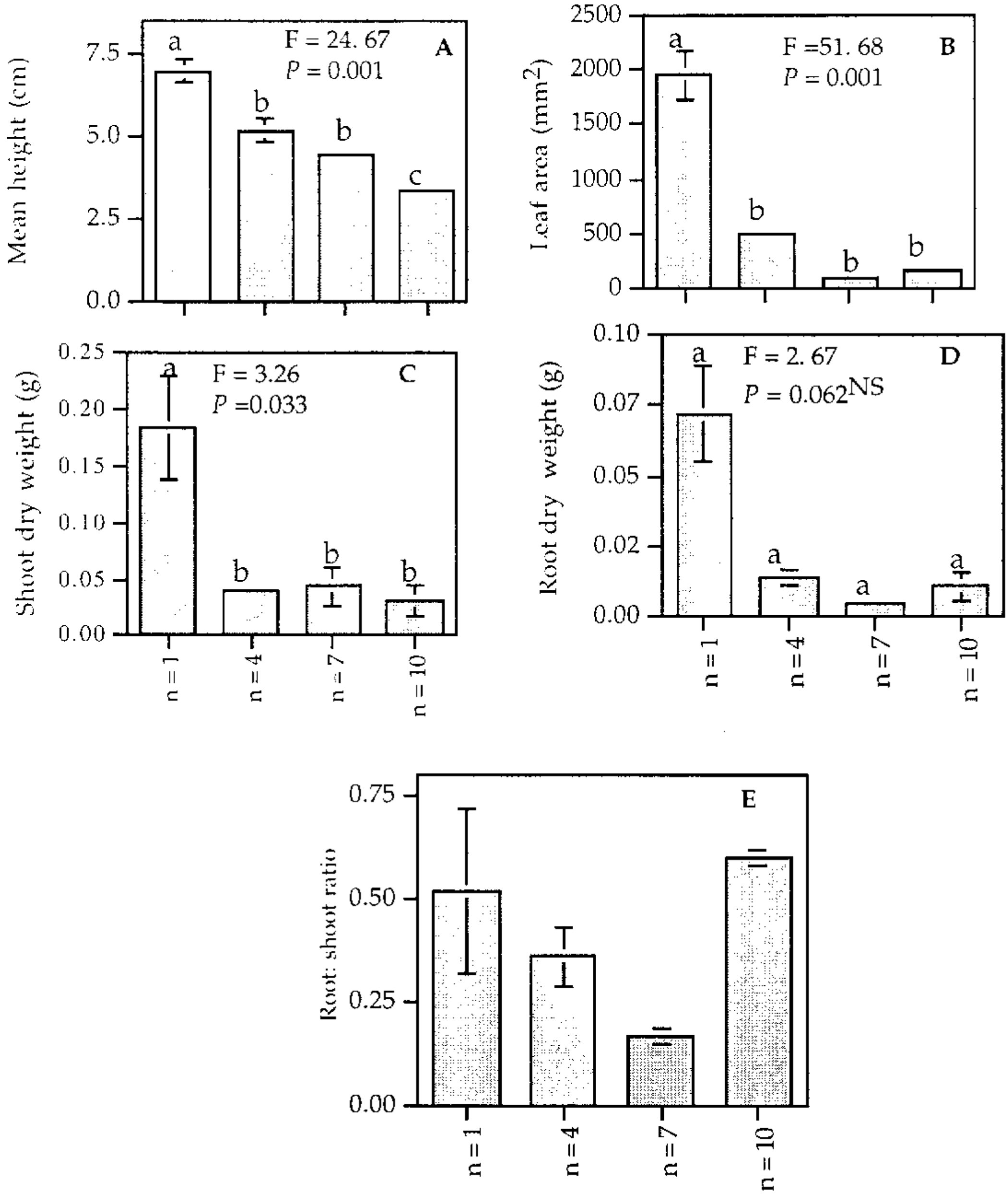


Figure 49: Mean harvest values of *E. victrix* seedlings at 9 wk, grown as monoculture in 140 mm (small) pots. Columns represent four densities, left to right where n=1 is control, one seedling per pot; n=4 is low, four seedlings; n=7 is medium, seven seedlings; and n=10 is high density, ten seedlings per pot. A) mean height (cm); B) leaf area (mm^2); C) shoot dry weight (g); D) root dry weight (g); E) root/shoot ratio. F and P are shown for analyses of variance for A to D. Bars are standard errors. Different letters indicate means are significantly different.

Mean shoot and root biomass of *E. victrix* seedlings (medium and large size pot) was significantly reduced at all densities (Figures 50 and 51 C and D).

Uncrowded seedlings, had larger leaf area than those grown at 4 or more per pot (Figures 49, 50 and 51). Differences were significant (P = 0.001) in all pot sizes. Control seedling leaf area was 2- 6 times larger in medium and large size pots than those grown in small pots. Leaf area tends to decline with increasing density and increase with pot size .

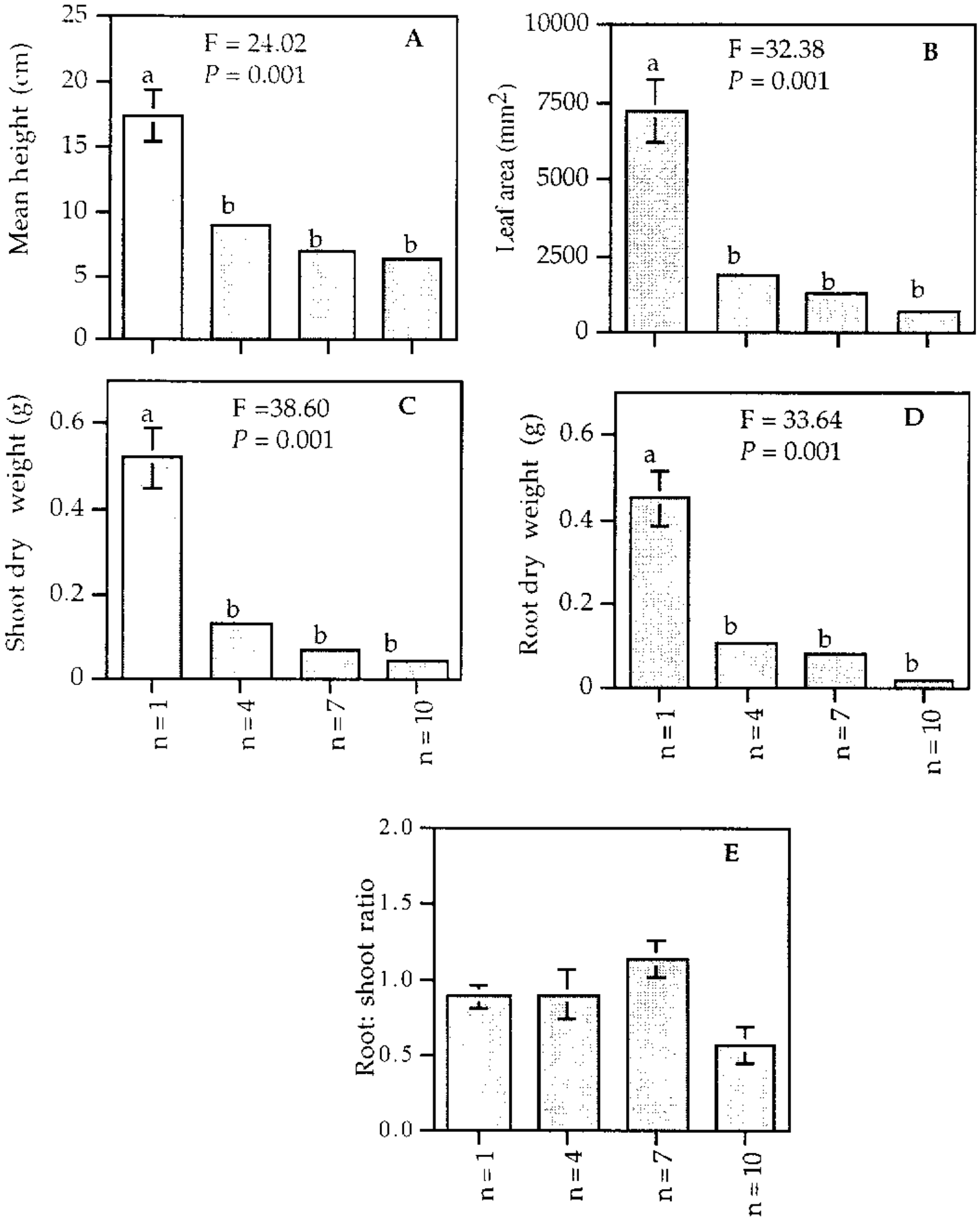


Figure 50: Mean harvest values of *E. victrix* seedlings at 9 wk, grown as monoculture in 200 mm (medium) pots. Other details as in Figure 49.

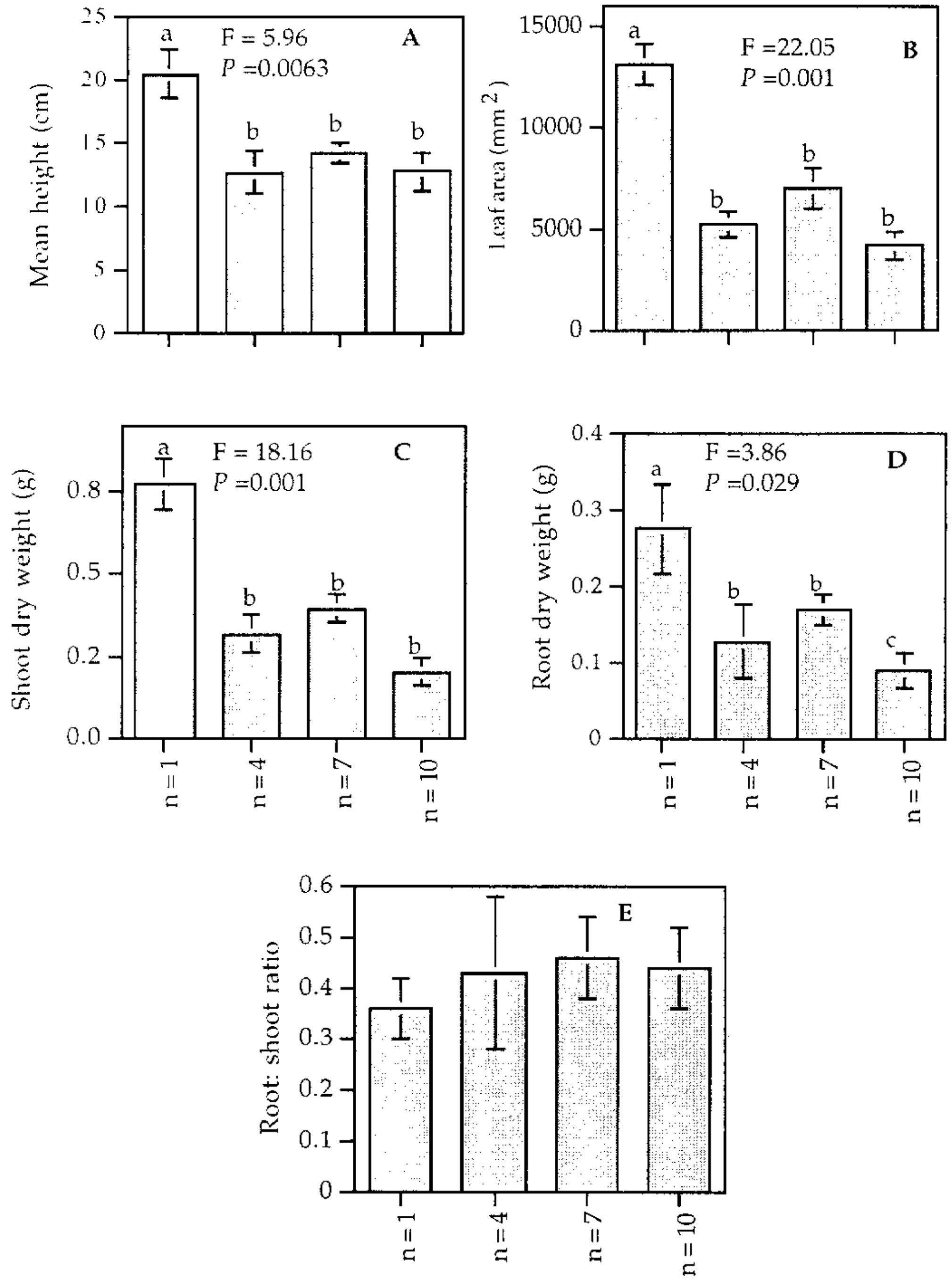


Figure 51: Mean harvest values of *E. victrix* seedlings at 9 wk, grown as monoculture in 250 mm (large) pots. Other details are as in Figure 49.

Mono culture versus mixed culture

Mixed culture

Analyses were performed with *E. victrix* seedlings as single plants in a pot (from the monoculture) with the mixed treatments (Figures 52, 53 and 54). Overall the monoculture seedlings had much greater growth in shoot height (except in small pots), root dry mass (except in small pot), and leaf area than seedlings grown in mixed culture. Comparisons between treatments in small pots (140 mm) revealed differences were not significant in shoot ($P = 0.28$) and root ($P = 0.20$) dry weight (Figure 52). In contrast, at medium (200 mm) (Figure 53) and large (250 mm) pot sizes (Figure 54), noticeable differences were observed.

A difference was observed in all measured parameters (except root : shoot) when *E. victrix* was planted before the grass in all pot sizes, this was more pronounced in medium and large size pots (Figures 52, 53 and 54). Treatment had a highly significant effect ($P = 0.001$) at all pot sizes (Table 25). Further, the mean comparison shows the treatment effect on leaf area. Leaf area was significantly larger when *E. victrix* was planted before grass in small, medium and large pot sizes, suggesting that root space availability is rapidly reduced (Figures 52, 53 and 54).

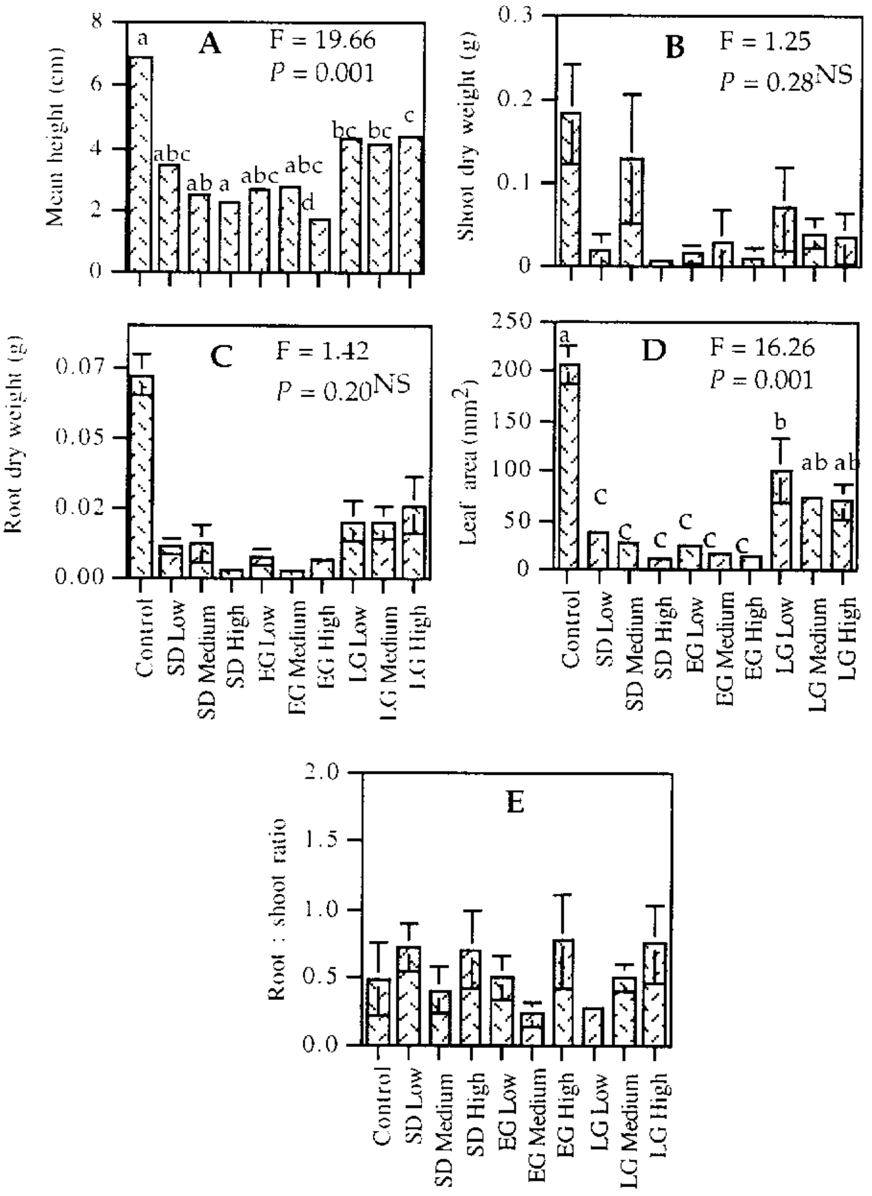


Figure 52: Mean harvest values of *E. victrix* seedlings at 9 wk, grown as monoculture compared with grass mixtures in 140 mm (small) pots. Control is *E. victrix* in monoculture; SD = mixture with grass and *E. victrix* planted together; EG = mixture with grass planted first; LG = mixture with *E. victrix* planted first. Low, medium and high refer to grass densities of 3, 6 or 9 plants per pot respectively. A) mean height (cm); B) shoot weight (g); C) root weight (g); D) leaf area (mm^2); E) root : shoot ratio. Vertical bars indicate standard errors. F= and P = are shown for analysis of variance for A to D. Same letters indicate means are not significantly different using Tukey's HSD test.

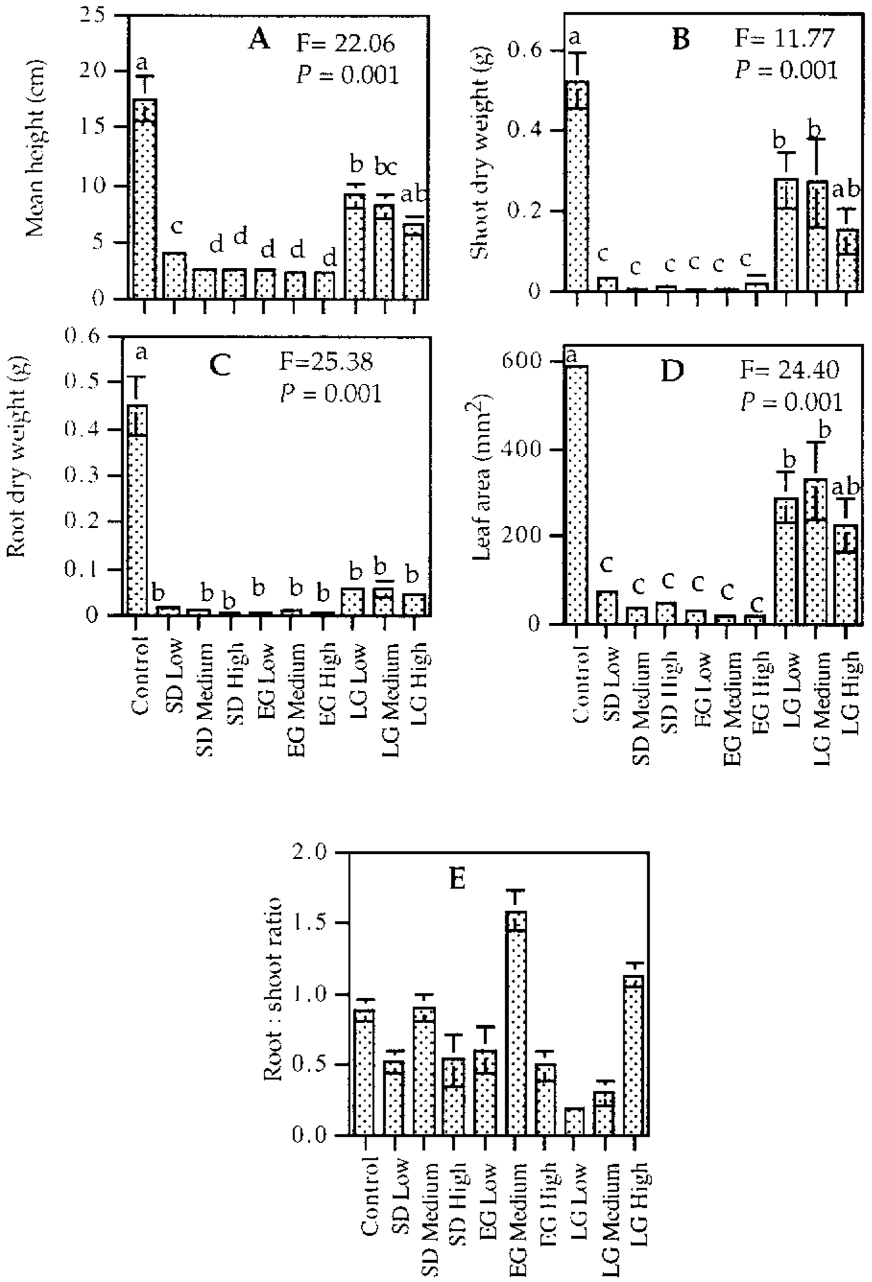


Figure 53: Mean harvest values of *E. victrix* seedlings at 9 wk, grown as monoculture compared with grass mixtures in 200 mm (medium) pots. Other details as in figure 52.

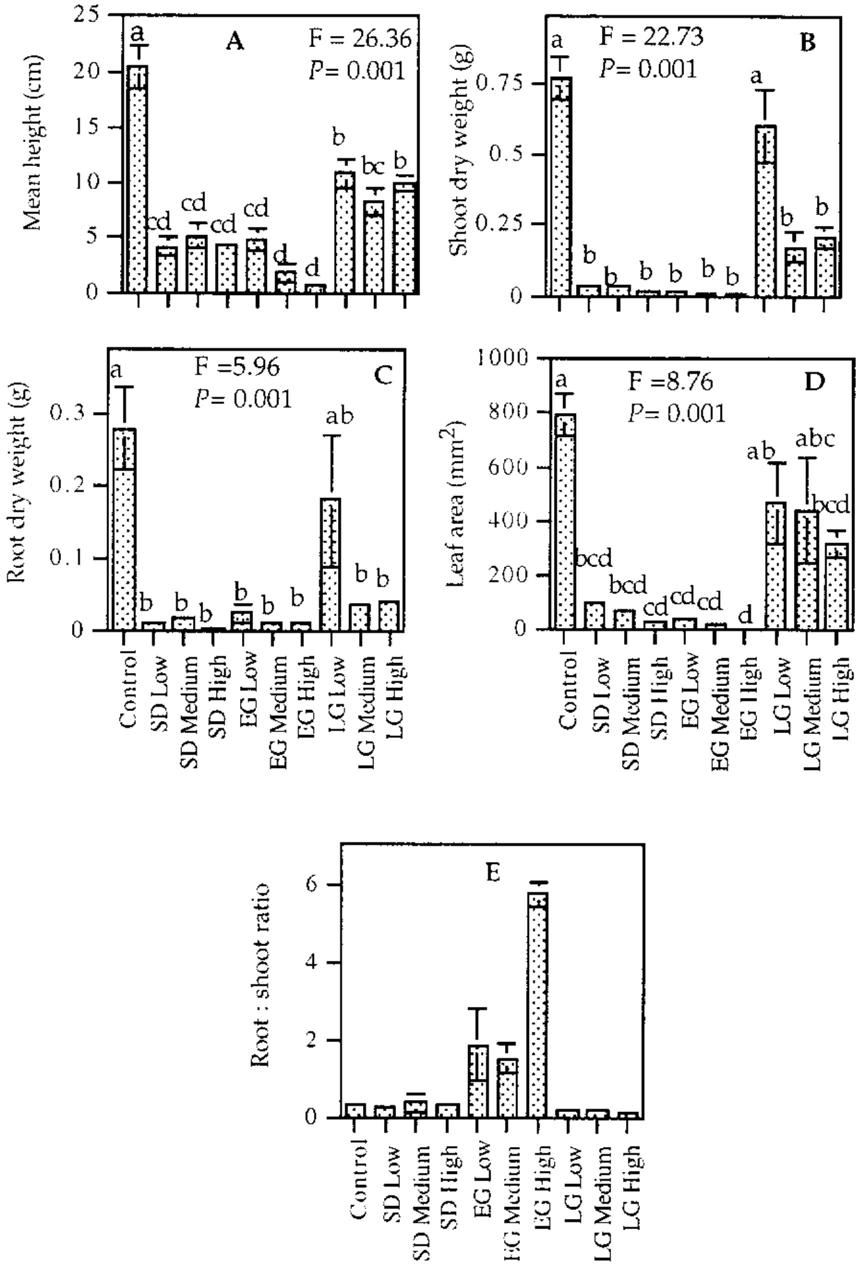


Figure 54: Mean harvest values of *E. victrix* seedlings at 9 wk, grown as monoculture compared with grass mixtures in 250 mm (large) pots. Other details as in figure 52.

Monoculture (ANOVA) analyses

Analysis of variance reveals that in monoculture there are highly significant differences (P = 0.001, after 9 wk) between seedling density levels, in each of: mean height; shoot dry weight; root dry weight; leaf area and number of leaves (Table 24). Similar differences are seen with available rooting volume (pot size). The interaction between density and rooting volume is also highly significant.

Table 24: Analysis of variance table for monocultures of seedlings of *E. victrix* .

Effect	df	Height (cm)			Shoot dry weight (g)			Root dry weight(g)		
		MS	F =	*P* =	MS	F =	*P* =	MS	F =	*P* =
D	3	257.79	36.99	***	0.716	49.10	***	0.225	30.24	***
P	2	706.70	101.40	***	0.816	55.95	***	0.239	32.05	***
D * P	6	38.81	5.60	***	0.080	5.51	***	0.070	9.43	***
Error	88	6.96			0.015			0.007		

Table 24 continued.

Effect	df	Number of leaves			Leaf area (cm^2)		
		MS	F =	*P* =	MS	F =	*P* =
D	3	66.32	21.49	***	2397.81	49.76	***
P	2	78.55	25.46	***	11525.14	239.19	***
D x P	6	10.95	3.55	**	1271.84	26.39	***
Error	88	3.08			48.18		

D = Density, P= Pot size, **$P < 0.01$; ***$P < 0.001$.

Mixed culture (ANOVA) analyses

Each of height, shoot and root dry weight, leaf area and total number of leaves attached to the seedlings at harvest, were analysed using two- and three-way analyses of variance for the mixed culture experiment (Table 25). *E. victrix* seedling height (cm) was very highly significantly different for each of pot size, time of transplanting and density. In two-way analysis, interaction between pot size and time was highly significant ($P = 0.001$). Three-way analysis of variance suggests a marginally significant interaction ($P = 0.05$) between pot size, time and density for seedling heights and dry weights (Table 25).

Table 25: Analysis of variance table for mixed cultures of grasses and *E. victrix*.

Effect	df	Height (cm)			Shoot dry weight(g)			Root dry weight(g)		
		MS	F =	*P* =	MS	F =	*P* =	MS	F =	*P* =
P	2	71.73	27.94	***	0.810	5.43	**	0.007	3.99	**
T	2	313.28	122.01	***	0.540	36.29	***	0.033	18.99	***
D	2	18.16	7.07	***	0.060	3.76	**	0.006	3.59	**
P x T	4	34.35	13.38	***	0.123	8.25	***	0.005	2.75	**
P x D	4	2.14	0.83	NS	0.035	2.33	**	0.005	2.72	**
T x D	4	1.28	0.49	NS	0.061	4.11	***	0.004	2.09	NS
P x T x D	4	6.37	2.48	*	0.031	2.07	*	0.004	2.16	*
Error	144	2.57			0.015			0.002		

Table 25 continued

Effect	df	Number of leaves			Leaf area (cm^2)		
		MS	F =	*P* =	MS	F =	*P* =
P	2	65.79	19.86	***	13.01	13.04	***
T	2	369.81	111.63	***	66.44	66.59	***
D	2	16.45	4.96	**	3.08	3.09	*
P x T	4	21.88	6.60	***	8.50	8.51	***
P x D	4	3.74	1.13	NS	1.04	1.05	NS
T x D	4	0.45	0.13	NS	0.66	0.66	NS
P x T x D	4	3.50	1.06	NS	1.10	1.10	NS
Error	144	3.31			0.99		

P= Pot size; T= Time of planting; D= Density of grass species;
* $P < 0.05$; **$P < 0.01$; ***$P < 0.001$. NS = Not significant.

Above and below ground biomass of mixed culture

E. victrix seedling shoot and root biomass varied significantly with main effects (pot size, establishment time and density) and also with different interactions (Table 25). Shoot weight differs significantly with pot size (P = 0.005) and density (P = 0.02). Root weight also differs significantly with pot size (P = 0.02) and density (P = 0.03). Highly significant (P = 0.001) differences were detected in time of transplanting for both shoot and root weights. The interactions between pot size and density and time and density suggest marginal differences between the competition effect on shoot and root biomass. Shoot biomass differs highly significantly with available root space and establishment time (Table 25). Similarly, a marginal difference was detected in above (P = 0.04) and below ground (P = 0.03) biomass in three-way interaction between rooting space, establishment time and density.

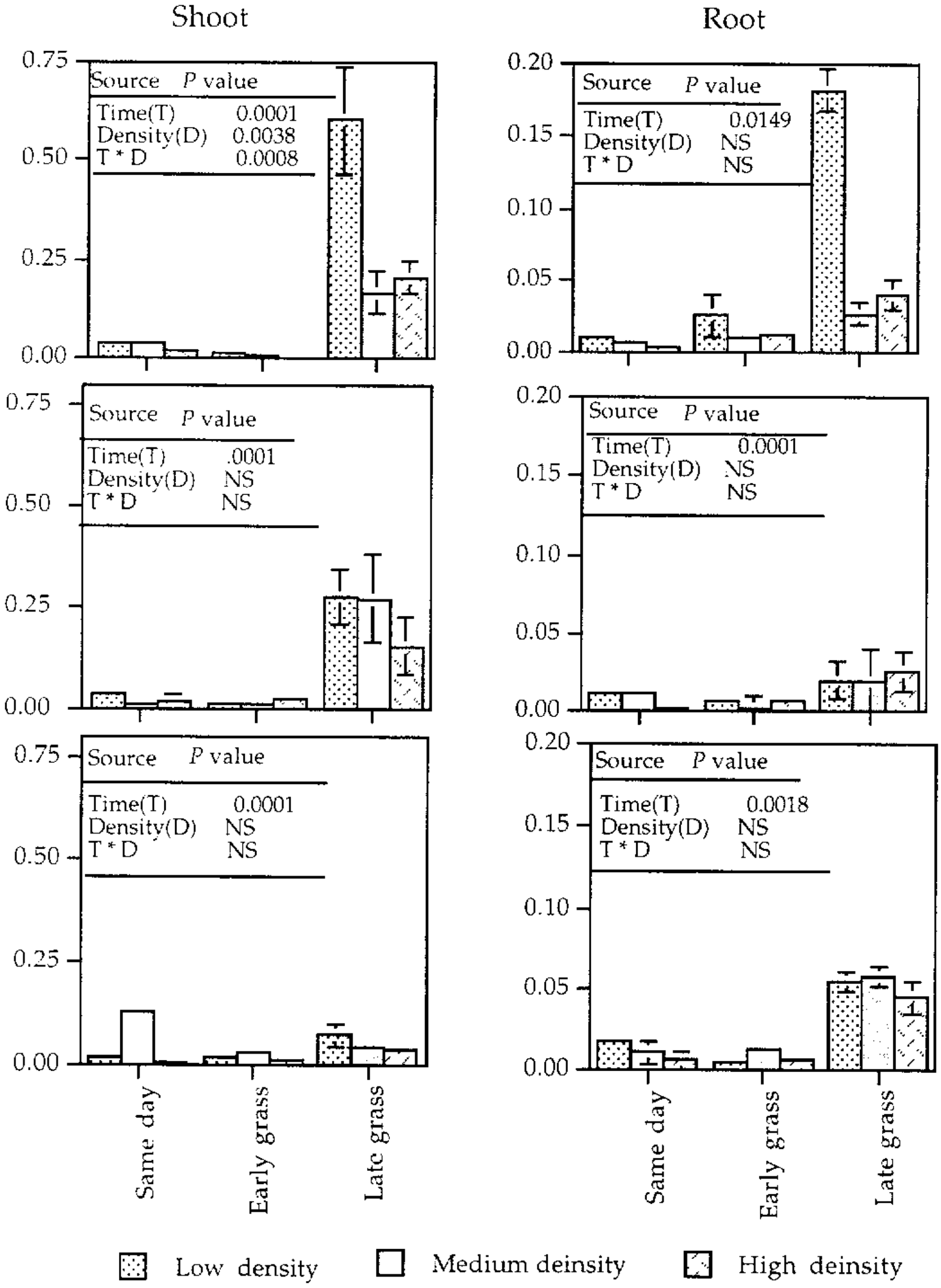


Figure 55: Shoot (left) and root (right) biomass of *E. victrix* seedlings in interspecific competition at 3 pot sizes: small (bottom), medium (middle) & large (top) size pots. Bars indicate standard errors.

Inter-specific competition

In grass competition, *E. victrix* seedling shoot and root dry weights are greatest when established before grass, at all pot sizes (Figure 55). Density appears to affect shoot weight only in largest pots (Figure 55).

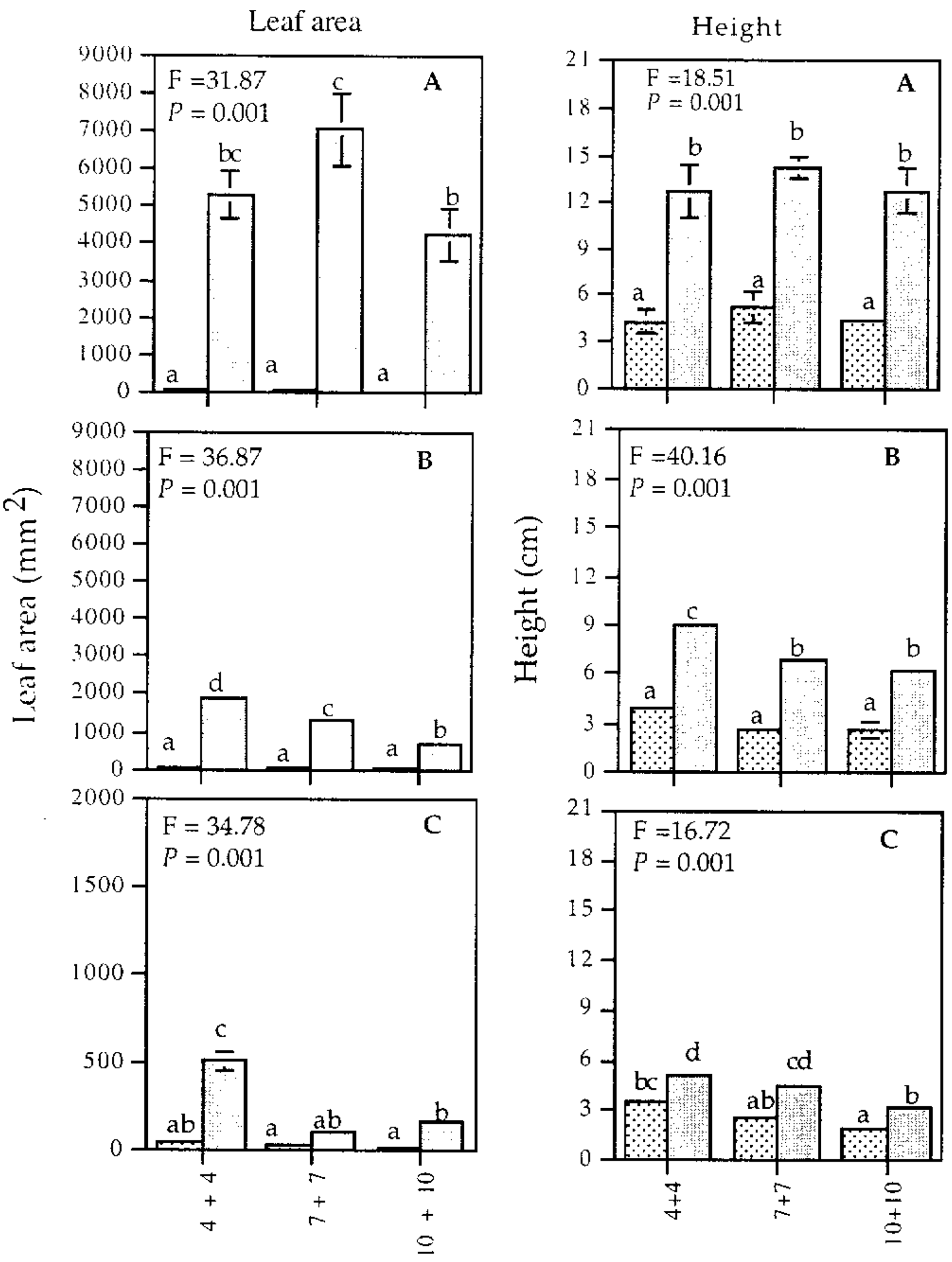


Figure 56: Difference between mixed stand (same day planting, stipple) *versus* monoculture stand (grey) leaf area (mm^2) and shoot height (cm) of *E. victrix* at different densities in different sized pots. Similar letters indicate means are not significantly different based on Tukey's HSD test. Bars indicate standard error. (**A**) Large pot, (**B**) Medium pot & (**C**) Small pot.

A comparison between monoculture and mixed culture with *E. victrix* established at the same time as the grass, shows *E. victrix* generally grows better in the pure stand. Differences for leaf area and height are highly significant at all pot sizes, except in small pot (7 + 7) density (Figure 56). In small pots, *E. victrix* height is suppressed with increasing grass density. This is not so in larger and medium pots. Leaf area of *E. victrix* with grass mixture is minuscule and significantly ($P = 0.001$) less than in monoculture for all treatments except small (7+7).

Discussion

The same moisture stimulus that promotes seedling recruitment of *E. victrix* (Chapter 2) also results in growth of annual herbage. As a consequence, fresh *E. victrix* seedlings are often concealed among grasses and other forbs (Figure 43). The species that germinates first will usually have a competition advantage. For some woody species it is necessary that they establish and grow before competing grasses, or that competing grasses are checked by grazing effects (Distel *et al.* 1996). During the period of growth associated with establishment, competition for resources (water, nutrients, light and space) may intensify as biomass develops. In the coolibah woodland, competition may be between *E. victrix* seedlings, neighbouring annual and perennial species, and also mature parent trees. Resources of importance are mainly soil moisture and rooting space. Competition for moisture is likely to become more intense as soils dry out. It was hypothesised that competition intensity from neighbouring grass species at differing densities would not be an important factor influencing mortality of newly recruited *E. victrix* seedlings. This is clearly not the case.

In general, seedlings of woody species rarely compete well with grasses (Van Auken and Bush 1988, Bush and Van Auken 1990). Most studies examine legumes or other relatively heavy-seeded woody species. This experiment sought to demonstrate the effect of grass species on seedlings of the relatively light-seeded *E. victrix*. The experiment clearly demonstrated that perennial and annual grass combinations at higher densities can severely restrict growth of *E. victrix* seedlings. Neighbouring grass seedlings have an early, measurable impact in suppression of shoot height and leaf area of *E. victrix* seedlings. An early reduction of shoot growth and leaf area of seedlings are symptoms of water stress (Hsiao and Acevedo 1974).

Tree species establishment is different when grasses are already established (Distel *et al.* 1996). Time of emergence also plays a major role in seedling mortality and growth in seedling populations. Earlier establishment of *E. victrix* seedlings in this experiment than the competing grass suggests that early germination of *E. victrix* could enhance subsequent growth and seedling survival, mainly through more rapid development of root mass. Early germinants would be superior competitors compared to later germinants (Fowler 1986).

Growth of the above ground part of the plant is dependent on the total surface area of the root. Root growth in turn depends on below ground conditions. Plants with similar root architecture tend to occupy similar soil levels. Annuals and perennials sharing the same ecological niche, have different growth rates and may exploit deferent parts of the soil profile. Annuals tend to finish their life cycle within a short period of time. As a result, they utilise all their available resources, generally near the surface soil, earlier than perennials. Root growth may be limited by one or the other type of plant, depending on the progress of seasonal growth.

In semi-arid environments both water and nutrients are at least seasonally, located in the surface horizon. As a result both tree and grass species tend to limit their roots within that zone (Scholes and Archer 1997). Competition for soil moisture between semi-arid plants is a major issue. When water is becoming a limiting factor to the below ground part of the plant, uptake of nutrients, particularly N, P and K is affected, because these nutrients enter by mass flow and diffusion (Sands and Mulligan 1990). Death of *E. victrix* seedlings in the field by early summer is clearly a combination of water shortage and lack of nutrients within the root zone.

Very few lateral roots were formed on seedlings in competition; they would have been limited by massive grass roots near the surface of the pot soil. *E. victrix* grown in monoculture produced more lateral roots (although these were thin) and long tap roots were observed. An ability to throw down a tap root during early development may give *E. victrix* an adaptive advantage in persisting through the first dry spring/early summer period. *E. victrix* root biomass was suppressed both in mixed culture and in monoculture. In mixture with grasses root growth was curtailed when *E. victrix* was established at the same time or later than the grasses but not when established earlier than grasses. Root competition from the grasses increased in magnitude as the available root space was decreased, similarly with increasing density of grasses. Root suppression in turn influenced shoot biomass of *E. victrix* seedlings.

Mortality of *E. victrix* was higher amongst those seedlings established as little as two weeks after the grasses. This demonstrates that early season root competition could be an important factor contributing to the death of *E. victrix* seedlings. The experimental results suggest that the effect of increasing neighbour density is to directly reduce biomass of *E. victrix* plants. This effect was observed in both mixed culture and in monoculture. The effect was more severe in mixed culture.

Timing of germination in *E. victrix* is apparently somewhat variable and depends on seasonal moisture availability. Grass establishment 2 weeks later tends to allow *E. victrix* seedlings enough time to establish control of resources compared with grass establishment before or at the same time as *E. victrix* seedlings. This may explain why a considerable number of *E. victrix* seedlings survived in a burnt grass land site (Chapter 2). There, *E. victrix* seedlings germinated into a site of no effective competition as a result of fire. Addition of extra nutrients from ash probably allowed seedlings to grow faster. In the experiment described in this chapter, higher leaf area of *E. victrix* was observed in monoculture than in mixed culture at all 3 levels of available rooting space. Density and shade both contribute competition stress affecting root development. Root competition was more intense than shoot competition. Disturbance by flooding or fire followed by a substantial amount of rainfall coupled with rapid, early germination would appear to permit ideal conditions for *E. victrix* seedlings to establish and grow and have low mortality rates.

Overall performance of *E. victrix* seedlings in this experiment suggests that single seedlings of *E. victrix* grow better and produce more biomass than more crowded plants, even if the crowded plants are grow more rooting space (i.e. large pots). This effect on growth of both above and below ground biomass results from competition for available resources in soil volume and other factors such as light. The pattern reflects poor competitive ability of *E. victrix* seedlings in the field.

This study confirms that seedlings of woody species do not compete very well with grasses. Field studies (Chapter 2) also demonstrate that *E. victrix* seedlings fail to establish with neighbouring grass species. It is suggested that early germination, before other species, would be an ideal condition for seedlings of *E. victrix* to establish and survive. Those *E. victrix* seedlings germinated after fire (Chapter 2) had a much lower mortality rate than seedlings germinated in sites with already established grasses and other annual (forbs) recruited after summer rain.

Finally, it should be pointed out that extrapolating from controlled experimental results to the natural condition should always be done with caution, since there are many biotic and abiotic factors that interact with each other in the field. Further, this study did not determine which grass species competes more effectively with *E. victrix* and for which resources these grass species are competing. Further experiments should be carried out in natural systems and these results presented in this chapter should be compared with the results presented in this chapter. However, this study is a first attempt to mimic natural conditions and to understand how newly recruited *E. victrix* seedlings compete with neighbouring grass species, available rooting space, time of establishment and also with adjacent with *E. victrix* seedlings.

CHAPTER 7

Evaluation of allelopathic effects of *E. victrix* on different plant species

Introduction

The term 'allelopathy' is derived from two Greek words 'allele' meaning mutual and 'path' meaning harm. The term allelopathy has been defined as any direct or indirect harmful effect by one plant (including micro organisms) on another through the production of chemical compounds released to the environment (Rice 1974). Putnam and Tang (1986) suggest allelochemicals may have inhibitory or stimulatory effects on neighbouring plant species. Allelopathy has been widely associated with *Eucalyptus* species (Al-Naib and Al- Mousawi 1976, del Moral *et al.* 1978, Putnam and Tang 1986, Shilling *et al.* 1992).

Many plants have been shown to contain toxins. Open woodland shows a sparse understorey (or suppression zone) associated with an allelopathic effect (Story 1967, del Moral and Muller 1970, del Moral *et al.* 1978, Lange and Reynolds 1981, Lamont 1985). It is also alleged that *Eucalyptus* affect both diversity and abundance of forbs and graminoids, and reduce the productivity of neighbouring crops by release of allelochemicals (May and Ash 1990). Lisanework and Michelsen (1993) examined the allelopathic potential of three *Eucalyptus* species namely: *E. globulus*, *E. camaldulensis*, and *E. saligna*, on seed germination, radicle growth and seedling growth of *Cicer arietinum* (chickpea), *Zea mays* (maize), *Pisum sativum* (pea) and *Eragrostis tef* (teff). Leaf extracts of all three species significantly reduced germination and radical growth in these crop species.

Several field and glasshouse studies on *Eucalyptus* species have demonstrated the release of volatile and water soluble toxins from *Eucalyptus* tissue. Al-Mousawi and Al-Naib (1976) found that reduction of herbaceous plants under the canopy of *E. microtheca* is not due to soil moisture, nutrients and shading but mainly due to phenolic and volatile compounds released from the foliage of *E. microtheca*. Anwar (1991) reported that extracts of (different concentration) fresh leaves, leaf litter and root tissue from *E. deglupta* and *E. alba* show phytotoxic effects against *Shorea palembanica* seedlings. Of the three different tissues the most toxic tissue is fresh leaf.

Several phenolic acids and volatile oils have been identified in different eucalypt species which are believed to be the major inhibiting substances released to the environment. Al-Mousawi and Al-Naib (1975, 1976) identified ß-pinene, camphene, - pinene and cineole from leaves of *E. microtheca*. From the same species Al-Naib and Al-Mousawi (1976) identified phenolic acids namely chlorogenic acid, isochlorogenic acid, ferulic acid, *p*-coumaric acid and caffeic acid that they also believe are part of the inhibitory substances produced by *E. microtheca* leaves. Hill and Isoi (1965) identified kaemperol, quercetin, ellagic, vanillic, gallic, ferulic, caffeic, chlorogenic and *p*-coumaric acids from *E. camaldulensis* leaves. Bignell *et al.* (1994) extracted pinene , 1,8-cineole and aromadendrene volatile oils from *E. incrassata, E. angulosa, E. ceratocorys, E. erythrandra, E. teraptera, E. forrestiana, E. dolichorhyncha* and *E. stoatei.*

Various studies have been carried out to examine allelopathic potential in controlled conditions. In general, aqueous extracts have been used to test allelopathic potential. The most used test species is *Lactuca sativa* L. (lettuce) as this is particularly sensitive to chemicals and uniformly germinates. Tests use leachate applied to potted seedlings or seeds. Sprayed whole leaf was used by del Moral *et al.* (1978) and powdered plant material by Bowman and Kirkpatrick (1986), Hytönen (1992), Waller (1993), Al - Mousawi and Al- Naib 1975). The powdered or chopped materials were soaked for certain time periods (Nishimura *et al.* 1982, Ahmed *et al.* 1984, Rao and Reddy 1984). In most cases aqueous extracts are obtained by soaking leaf, bark, root or litter (collected under the test tree species) for 15 to 24 hours (del Moral and Mueller

1970, Heisey and Delwiche 1985, Lamont 1985, Bowman and Kirkpatrick 1986, Kohli *et al.* 1988a and b, Zhang 1993, Pellissier 1994, Macias *et al.* 1996, Adkins and Sowerby 1996). Some allelopathy studies used leachate from soil collected under the suspected tree (Kohli and Singh 1991). Ferguson (1991) studied volatile compounds using control chambers allowing the volatile compounds to pass through the seed.

Del Moral and Muller (1970) demonstrated that extracts of fresh leaves from *E. camaldulensis* were more toxic to *Bromus rigidus* seeds than bark, litter and root. Al-Mousawi and Al-Naib (1975) claim that phytotoxicity effects are higher from old brown leaves than young green leaves of *E. microtheca*. Bowman and Kirkpatrick (1986) show that dry leaf extract of *E. delegatensis* inhibits its own germination and reduces hypocotyl growth. Singh *et al.* (1991) suggest that oil extracted from *E. citriodora* and *E. globulus* retards growth of *Phaseolus aureus* Roxb. Shilling *et al.* (1992) claim celery root tissue has a greater impact on *L. sativa* shoot weight and root weight than celery petiole and lamina tissue.

In the Fortescue valley, *E. victrix* foliage and bark debris may accumulate under large trees in those years with little rainfall. It is hypothesised that organic compounds present in such litter may possess antibiotic properties. This may have an adaptive advantage as seedling germination may not become established in the absence of adequate soil moisture. Therefore it would be worthwhile to examine whether there is any allelopathic effect of *E. victrix* on surrounding vegetation. The main objective of this preliminary work is to evaluate potential allelopathic effects of *E. victrix* on native grasses and two eucalypts species (*E. terminalis* and *E. leucophloia*).

Hypotheses

i] Germination of *L. sativa* is not affected by water soluble extracts from *E. victrix* foliage and bark.

ii] Growth of *E. victrix, E. microtheca, E. terminalis* , *E. leucophloia* and the grass species: *S. dielsii, P. adecompositum* and *Leptochloa digitata* is not affected by leaf leachate from *E. victrix*.

Experiment I - Germination bioassay

Method

Fresh leaves and bark from several trees of *E. victrix* were collected in coolibah woodland in the Fortescue valley floodplain. These samples were brought to Perth and separately ground in a grinder (Retsch Gmbh WRS 80 c/29). Ground materials were kept in dark bottles until used. Using procedures adapted from Tian and Kang (1994), aqueous extracts of *E. victrix* leaves and bark were prepared by shaking (Griffin flask shaker) 30 g of ground material with 240 mL of deionised water (1:8 weight) in 500 mL flasks for 2 hr at room temperature. The solutions were filtered into separately labelled flasks, using No. 3 Whatman® filter paper (125 mm) and stored at 5°C until used.

Leaf leachate was prepared by soaking 30 g of air dried leaves in 240 mL of deionised water for 24 hours. Leachate was filtered using No. 3 Whatman® filter paper (125 mm) and stored at 5°C.

Following filtering, three different concentrations were prepared from each of the ground bark extract, ground leaf extract and leaf leachate.

i] Control, 100% deionised water

ii] 100% fresh extract or leachate (1: 8 weight).

iii] 75% of extract or leachate and 25% deionised water.

iv] 50% of both extract or leachate and deionised water.

In this initial test, *L. sativa* 'Great Lakes' seeds were used, mainly for their uniform germination (Dietz and Winterhalter, 1996) and sensitivity to germination inhibitors (Evenari and Newman 1952). Sets of 4 replicates of 50 seeds were sown in petri dishes on 9 July 1997. The basal part of the petri dish was covered with sterilised vermiculite and two layers of No. 3 Whatman® filter paper were placed on the vermiculite. Filter paper was moistened with 10 mL of aqueous extracts of different treatments. Petri dishes were labelled and placed in a 25°C growth cabinet. These petri dishes were kept continuously moist until the experiment was terminated (25 days). Seed germination and radical length were recorded from 24 hours after the onset of germination.

Statistical analyses

Germination data were transformed by arcsin to normalise the data and then analysed using analysis of variance with super ANOVA™ software program (Abacus Concepts, Berkley, Califonia).

Results

Full strength bark and leaf extract solutions and leaf leachate dramatically decreased germination of *L. sativa* seeds. The effect was most pronounced with all three solutions of leaf extract as the full, medium and low strength solutions resulted in only 5, 9 and 12% seeds germinated respectively, compared to 98% germination of the control seeds. Bark extract gave a progressively greater effect as strength was increased compared to control as did leaf leachate (Figure 57).

Table 26: Analysis of variance of *L. sativa* seed germination at 25 day.

Source	df	Sum of square	Mean square	*F* value	Significance
Solutions [S]	3	0.014	0.005	25.27	0.001***
Plant tissues [Pt]	2	0.017	0.008	45.27	0.001***
S x Pt	6	0.006	0.001	5.50	0.001***
Residual	36	0.007	0.000194		

Significant differences are indicated *** $P < 0.001$.

Leaf leachate produced higher germination rates at the medium concentration than at the lower solution (Figure 57). There was a significant interaction between solutions and plant tissues (Table 26).

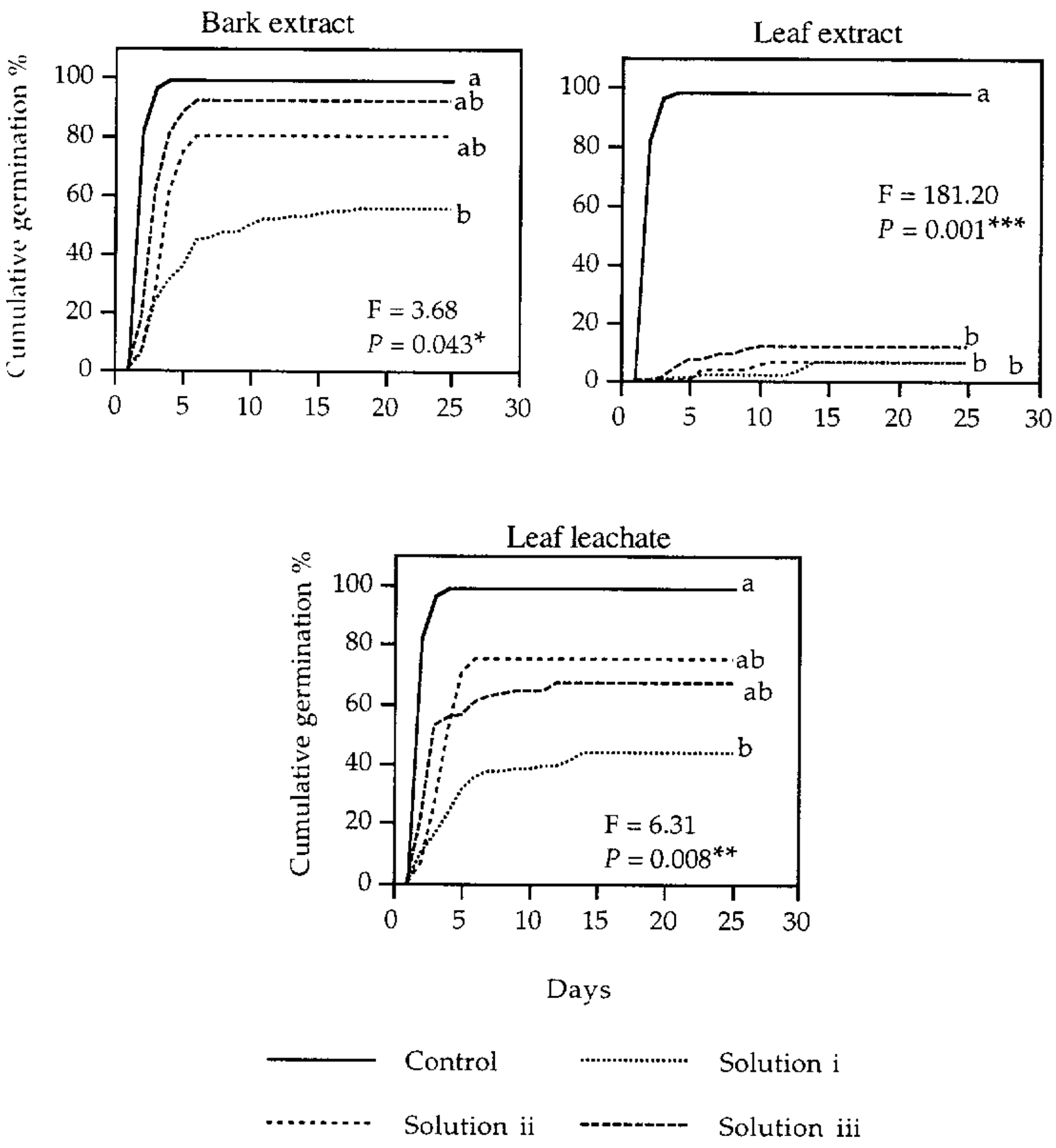


Figure 57: Germination of *L. sativa* seed subjected to *E. victrix* leaf and bark leachate and leaf extract. Significant differences are indicated $^{*}P< 0.05$; $^{**}P< 0.01$, *** $P < 0.001$; Same letters are not significantly different ($P < 0.05$) as determined by Tukey's Pairwise comparison. Control = only deionised water; solution i = 100% fresh extract or leachate; solution ii = 75% of extract or leachate and 25% deionised water and solution iii = 50% of both extract or leachate and deionised water.

Phytotoxic effects were also observed on seed radicle length. All three solutions and concentrations caused a significant reduction in growth (Figure 58). However, there was no significant interaction between solutions and plant tissues (Table 27). It was also observed that the radicles became brown at the collar. Eventually the whole radicles became dark brown and led to death of the seedlings during the period of the experiment .

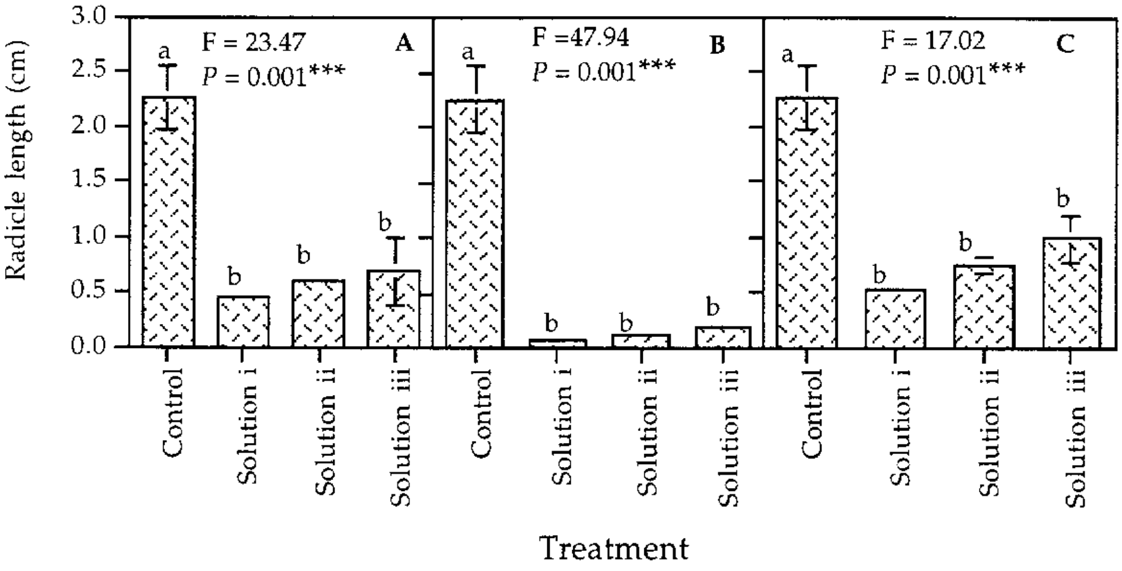


Figure 58: The effect of aqueous extract from (A) bark and (B) leaf and leaf leachate (C) on *L. sativa* radical length. Treatments with same letters are not significantly different ($P < 0.05$) as determined by Tukey's Pairwise comparison (SE indicated). Control = only deionised water; solution i = 100% fresh extract or leachate; solution ii = 75% of extract or leachate and 25% deionised water and solution iii = 50% of both extract or leachate and deionised water.

Table 27: Analysis of variance table for *L. sativa* radicle length (cm).

	df	Sum of squares	Mean square	F value	Significance
Solutions [S]	3	29.25	9.75	80.257	0.001^{***}
Plant tissues [Pt]	2	2.001	1.00	8.234	0.001^{***}
S x Pt	6	0.782	0.13	1.072	0.397^{NS}
Error	36	4.374	0.12		

Significant differences are indicated *** $P < 0.001$. NS = not significant.

Experiment II - Plant growth with leachate

Method

Seeds of *E. victrix*, *E. leucophloia* and *E. terminalis* and the grasses *P. decompositum*, *S. dielsii* and *L. digtata* were collected from Newman, in February 1997 and stored in air tight bottles at room temperature until use. *E. microtheca* seeds were obtained from The Sudan Forestry Department. Potting soil was collected away from *E. victrix* trees in coolibah woodland. Soil was sieved through a wooden sieve (diameter 48.5 cm, mesh size 2.0 mm) to remove larger plant parts and stones. Seeds were sown in trays of sterilised coarse sand trays on 14. 06. 1997. Sets of 35 uniform sized seedlings were transplanted (01. 08. 1997) into pots (45 mm diameter and 170 mm tall) filled with the coolibah woodland soil. Transplanted seedlings were kept in a glass house for three weeks to acclimatise. Rain water was added as required. Any dead seedlings were replaced during this period.

Leaves and small twigs of *E. victrix* were collected from healthy trees near Newman and stored in a cool box, transported to Perth and kept in a freezer until use. Leaf leachate was prepared by soaking 140 g of leaves in 7 L of rain water for 20 hours (Lamont 1985). Leachate was then filtered through a hand strainer and stored at 5°C. Fresh solutions of leachate were prepared when necessary.

The experiment was set up as a randomised design and three treatments were applied. Treatment 1 was leachate diluted 1:1 with rainwater; treatment 2 was undiluted leachate; treatment 3 was the rain water control. Sets of 10 replicates of each species were randomly assigned to treatments, labelled with coloured plastic tags and treated with 10 mL of the appropriate solution thrice-weekly from 08. 08. 1997 to 17.10. 1997.

After 8 weeks (17. 10. 1997), all seedlings were harvested. Plants were washed in tap water and placed in separately labelled bags. Seedlings were then dried at 105°C for 24 hours and shoot and root dry weights were obtained separately using an electronic balance.

Statistical analyses

Data were analysed using Super ANOVA soft ware program (Abacus Concepts, Berkley, California) for one-way ANOVA. Residual plots of each ANOVA were obtained to examine homogeneity of variance. Based on residual plots, data were transformed to log, square or arc sin as appropriate and reanalysed. The data presented here are of uniform means.

Results

Allelopathic properties are indicated by the results (Tables 28 and 29). Among the eucalypts leachate generally depressed both mean shoot and root growth when compared with rainwater. Exceptions were shoot growth of *E. leucophloia* which was not affected (Table 28 and 29). Undiluted leachate tended to depress shoot growth more than half strength leachate in *E. victrix*, *E. microtheca* and *E. terminalis*. There was no difference between undiluted and half strength leachate on root dry weight.

Differences between treatments were significant and attained weights were similar in *E. microtheca* and *E. victrix*. In these closely related species, leachate appeared to reduce shoot growth more than root growth. In both *E. leucophloia* the differences between treatments were not significant for either shoot or root growth. Shoot growth of *E. terminalis* was affected while root growth was not. Mean shoot growth in *E. leucophloia* appeared to be greater than all other species for all three treatments (Table 28).

Table 28: Mean shoot dry weight ± SD (g) of different test species at 8 week. (n= 10). Control = only deionised water; solution i = leachate 1:1 diluted and solution ii = undiluted leachate.

Species	Control	Solution i	Solution ii	F	Significance
E. victrix	0.060 ± 0.018^{a}	0.039 ± 0.011^{b}	0.025 ± 0.011^{c}	17.08	***
E. terminalis	0.093 ± 0.050^{a}	0.094 ± 0.027^{a}	0.068 ± 0.018^{b}	0.006	**
E. leucophloia	0.286 ± 0.126^{a}	0.214 ± 0.086^{a}	0.188 ± 0.107^{a}	2.23	NS
E. microtheca	0.068 ± 0.031^{a}	0.045 ± 0.010^{b}	0.019 ± 0.014^{c}	14.37	***
P. decompositum	0.074 ± 0.019^{a}	0.047 ± 0.015^{b}	0.033 ± 0.011^{b}	18.24	***
S. dielsii	0.078 ± 0.017^{a}	0.062 ± 0.023^{ab}	0.055 ± 0.020^{b}	3.41	*
L. digitata	0.046 ± 0.22^{a}	0.025 ± 0.009^{b}	0.013 ± 0.006^{b}	14.39	***

Means followed by the same letters are not significantly different *P< 0.05; **P< 0.01, *** P < 0.001; as determined by a Tukey's Pairwise comparison. NS = Not significant.

Among the grass species, *S. dielsii* had heaviest mean shoot weight, *P. decompositum* (Figure 59) greatest root weight and *L. digitata* generally produce least shoot or root weight. Significant differences were obtained in shoot and root weights for grasses except for root weight in *S. dielsii* (Table 29).

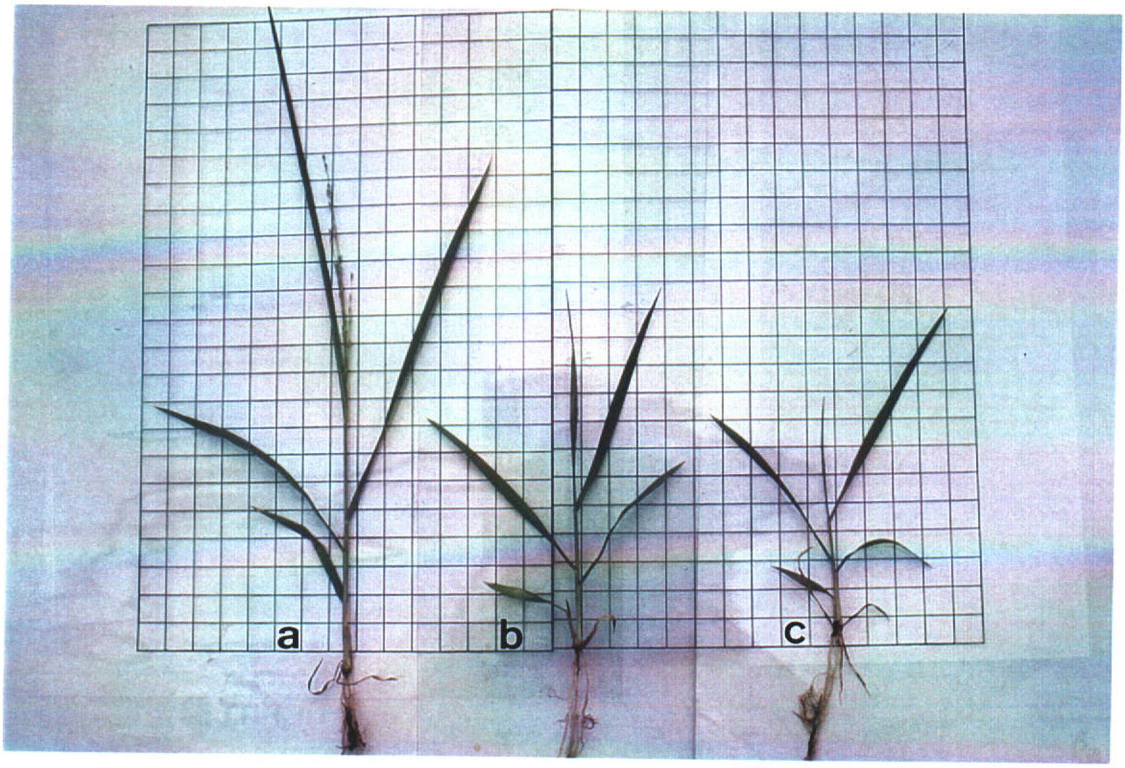


Figure 59: Shoot growth in *P. decompositum*. a - treated with rain water (control); b- 50% leachate + 50% rain water; c - 100% leaf leachate. [grid is 1 x 1 cm].

Table 29: Mean root dry weight (±SD) of different test species. n= 10. Control = only deionised water; solution i = leachate 1:1 diluted and solution ii = undiluted leachate.

Species	Control	Solution i	Solution ii	F	Significance
E. victrix	0.036 ± 0.020^{a}	0.017 ± 0.005^{b}	0.014 ± 0.008^{b}	8.99	**
E. terminalis	0.045 ± 0.027^{a}	0.044 ± 0.024^{a}	0.036 ± 0.020^{a}	0.46	NS
E. leucophloia	0.055 ± 0.020^{a}	0.064 ± 0.045^{a}	0.039 ± 0.018^{a}	1.66	NS
E. microtheca	0.035 ± 0.011^{a}	0.017 ± 0.006^{b}	0.021 ± 0.012^{b}	8.16	**
P. decompositum	0.062 ± 0.030^{a}	0.043 ± 0.020^{ab}	0.033 ± 0.011^{b}	4.52	*
S. dielsii	0.035 ± 0.017^{a}	0.028 ± 0.024^{a}	0.025 ± 0.014^{a}	0.73	NS
L. digitata	0.040 ± 0.026^{a}	0.019 ± 0.009^{b}	0.009 ± 0.004^{b}	10.06	***

Means followed by the same letters are not significantly different $^{*}P< 0.05$; $^{**}P< 0.01$, *** $P < 0.001$; as determined by a Tukey's Pairwise comparison. NS = Not significant.

Experiment III - Evaluation of phenolic compounds from *E. victrix* leaf and bark extracts

Method

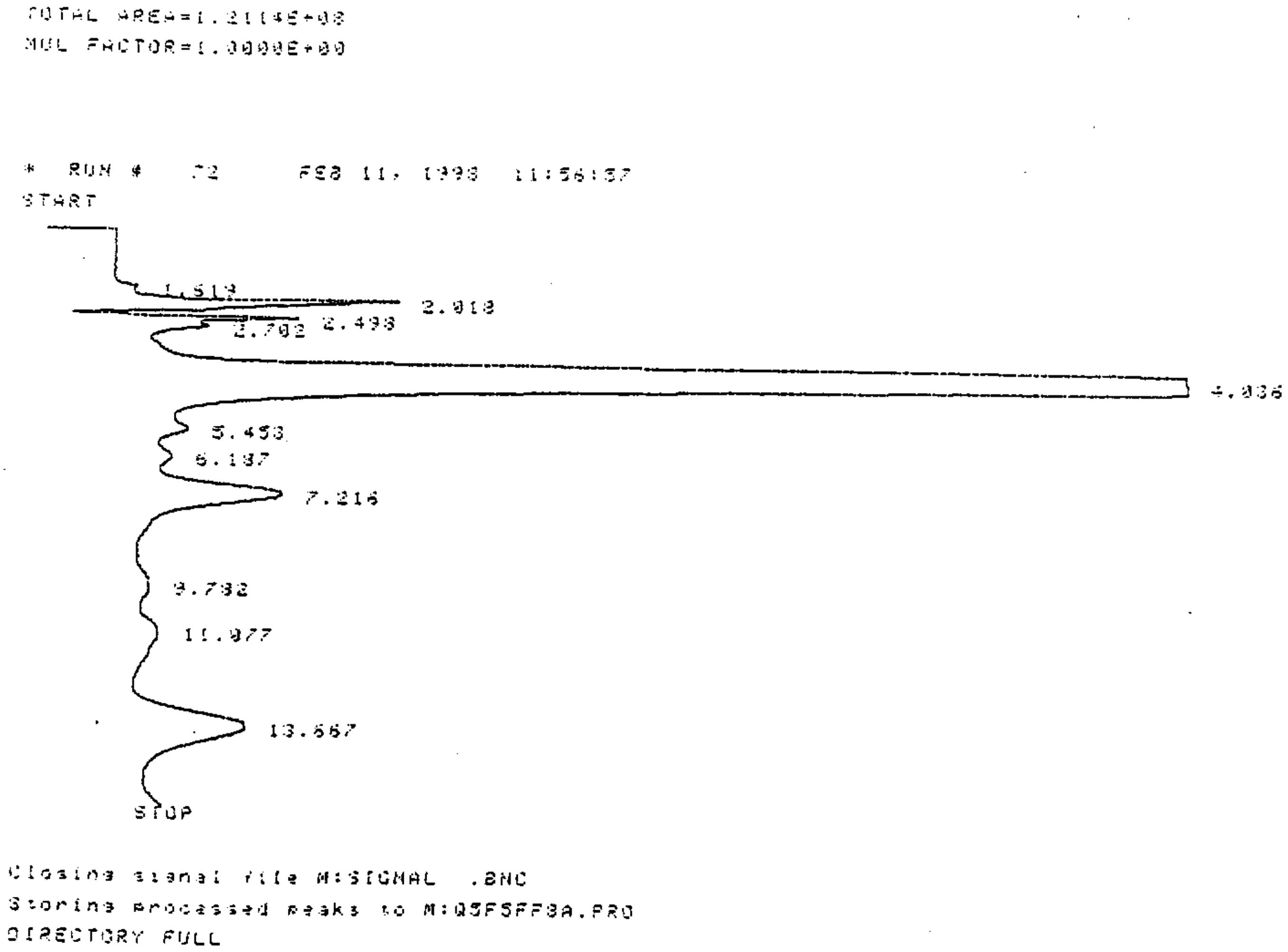
To quantify the presence of allelopathic substances (phenolics), *E. victrix* leaves and bark were collected from healthy trees in Newman, Pilbara during September 1997. They were stored in a cool box in the field and transported to Perth and then stored in a freezer until use. Thirty grams of leaves and bark were sliced into approximately 1 cm pieces and placed in 500 mL beakers containing 240 mL of distilled water. Both beakers were heated to boiling point and left to cool down over night (at room temperature). Solutions were then filtered using Whatman® No 1 filter paper (24 cm) and collected in 500 mL conical flasks. Extracts were acidified to pH 2.5 with HCl and diluted to half volume with diethyl ether. The fraction was evaporated to dryness *in vacuo* for 15 to 20 minutes. Residues of 0.280 and 0.208 g leaf and bark were taken in 10 mL of absolute methanol (CH_3OH) (Al- Naib and Al-Mousawi 1976). Solutions were used in high performance liquid chromatography (HPLC). An Econosil reverse phase column c18, (10 µ 250 x 4.6 mm) was used for this analysis. (supplied by Alltech). Dioxane-2% HOAc (15 : 85) was used as a mobile phase with UV detection at 280 nm (Roger *et al.* 1986).

Results

Chromatography and spectrophotometric analyses of leaf and bark extracts were performed. Based on the peak (absorption/retention time) possibly eleven and eight phenolic compounds were observed from bark and leaf respectively (Figure 60, 61 and Table 30).

Table 30: Absorption time of possible phenolic compounds from the leaf and bark of *E. victrix*.

Phenolic compounds	Absorption time (Min)	
	Bark	Leaf
i	2.702	2.519
ii	4.036	4.018
iii	5.458	6.551
iv	6.187	7.516
v	7.216	9.975
vi	9.782	9.975
vii	11.077	11.845
viii	13.667	14.589
ix	-	18.569
x	-	25.330
xi	-	29.296



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MUL FACTOR=1.0000E+00


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Figure 60: High performance liquid chromatography for *E. victrix* bark extract.

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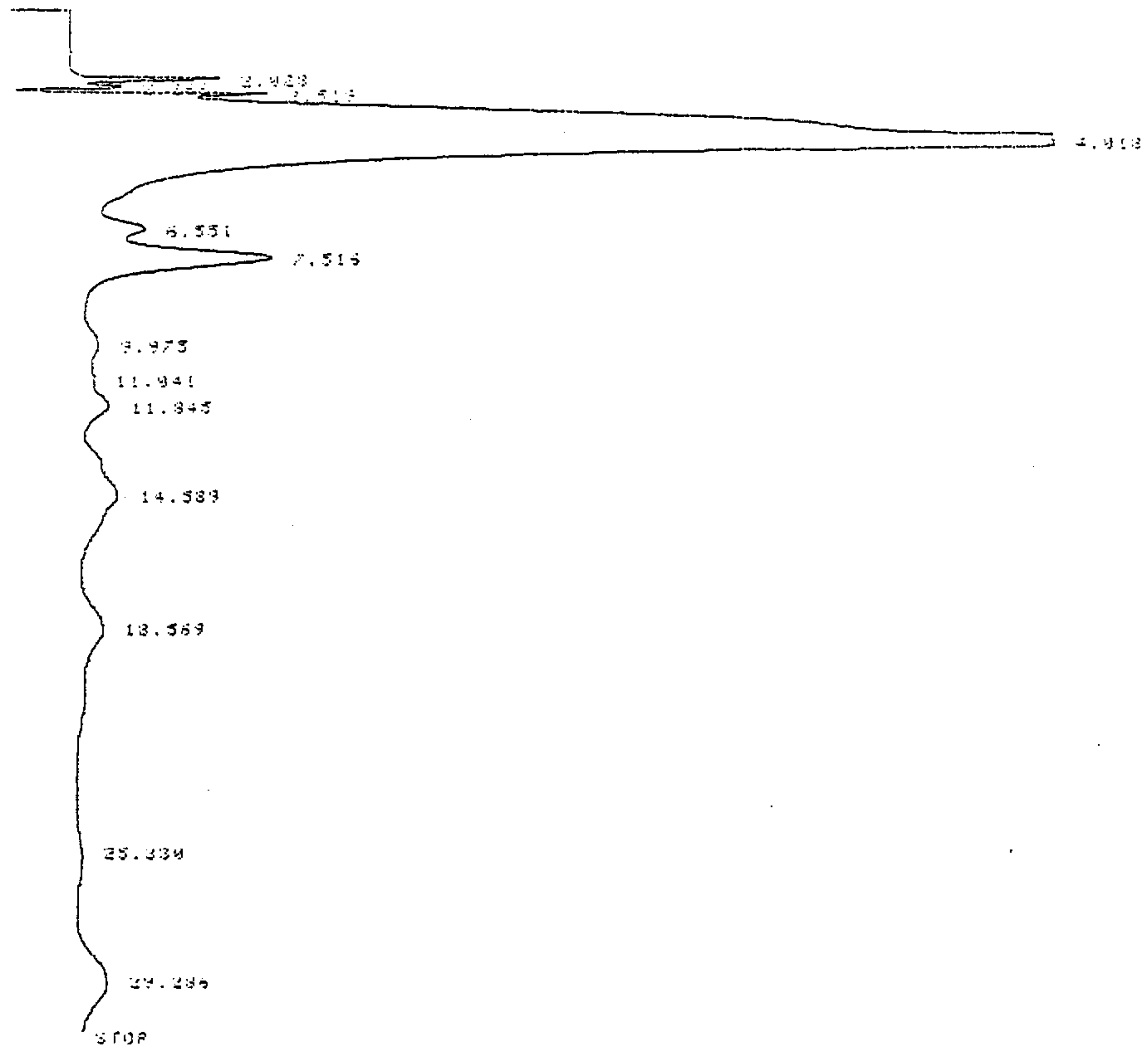

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Figure 61: High performance liquid chromatography for *E. victrix* leaf extract.

Discussion

E.victrix leaf extract has a major effect on *L. sativa* seed germination. Bowman and Kirkpatrick (1986) suggest such extracts may have higher osmotic concentrations than leachates. The most concentrated solutions of bark extracts and leaf leachate from *E. victrix* show a considerable inhibition of *L. sativa* seed germination. Different inhibitory effects from different parts of the same plant are likely due to variation in the amount of phytotoxic compounds produced from different plant tissues (Rice 1974, Putnam and Tang 1986, May and Ash 1990).

Leaf leachate for *E. victrix* depressed growth in a range of species trialed but results were not universally effective and in several cases the effect of leachate was not significant. Shoot and root growth of *E. victrix* and *E. microtheca* were affected significantly by leaf leachate. The growth (shoot and root) of grasses was also affected to different degrees when treated with leaf leachate.

This leachate effect has relevance to the previously described experiment on the grass/ tree association (Chapter 5). This trial suggests that *E. victrix* leaf leachate has an inhibitory effect on the tested grass species but not on the local eucalypt species, *E. terminalis* and *E. leucophloia*. Leaf leachate does have a major impact on *E. victrix* and *E. microtheca*. Bowman and Kirkpatrick (1986) found *E. delegatensis* forest litter and roots do not inhibit germination or growth of its own seedlings, but leaf extract significantly reduces germination and hypocotyl growth of seeds when compared to control treatment (distilled water).

In the field, soil concentration of potential allelochemicals depends on the amount of material shed from trees, the accumulation of alleochemicals in the soil. The soil water balance is correlated with rainfall events. Lower rainfall implies higher allelochemical concentration beneath the canopy area (May and Ash 1990). The concentration of allelochemicals is reduced dramatically after rain in *E. camaldulensis* woodland in California (del Moral and Muller 1970).

Further, potential allelochemicals may bind with soil colloids or be broken down by bacteria, decreasing concentrations in open systems (Rice 1974).

A number of possible phenolic compounds extracted from leaf (11) and bark (8) of *E. victrix* were noted; further examination is required to evaluate potential effects on seed germination of native grasses and forb species.

Preliminary results suggest that *E. victrix* contains water soluble phenolic compounds in leaf, bark and litter. These solutes are capable of reducing the germination of *L. sativa* seeds. Growth of four eucalypt species and three native grass species was variably affected. This may explain at least in part, why *E. victrix* trees are often devoid of ground cover beneath their crown.

CHAPTER 8

Seed longevity of *E. victrix* in the field

Introduction

The habitat in which *E. victrix* occurs is climatically harsh being subject to high temperatures and sporadic summer rainfall. It was observed that *E. victrix* trees complete their phenological cycle within a short period of time (about 3 months). Mature fruits open and shed seed and chaff (aborted ovules) after the summer rain. When seed falls on moist soil a large number of new recruits may establish. On some occasions, seeds of *E. victrix* are shed during hot, dry summer conditions when germination may not be suitable. No *E. victrix* seedlings have been germinated from soil collected from the coolibah woodland (Graham, 1998). The aim here was to discover the fate of shed seed during prolonged dry conditions. Yates (1995) found with *E. salmonophloia,* that low rainfall and low humidity during summer prevent seeds from germinating. Further, small seeds like *E. victrix,* are likely to be damaged by the high ambient temperatures, eaten or damaged by predators or damaged by microbes.

Many eucalyptus species are serotinous with above ground (on plant) seed banks (Parker and Kelly, 1989). Stoneman and Dell (1994) found that 90% of *E. marginata* seed is removed by vertebrates or invertebrates after release from the capsule. It is possible that some newly shed seeds of *E. victrix* may be removed by ants.

The main objective of this study was to examine how long seed remains viable in soil after release from capsules. It was hypothesised that most field germination and establishment follows current seed fall (seed rain) into moist soil. Seed may be lost by flooding after seed fall and by a range of possible environmental factors resulting from seed falling onto dry ground and failing to germinate immediately.

Hypotheses

1] There is no difference in *E. victrix* seed longevity between a control and 94 and 142 days after burial.

2] There is no difference in seed longevity between seed buried beneath the canopy of *E. victrix* (shade) or open gaps.

Methods

Burial and removal techniques with seed bags (Lunt 1995) were used to examine the longevity of seeds of *E. victrix*. A burial depth of 50 mm was used, as *Eucalyptus* seeds buried between 0.50 and 50 mm depth tend to have higher germination than when placed above or below these depths (Ashton 1979, Stoneman and Dell 1993, Grant and Bell 1994). Seed bags were not left on the soil surface, mainly because in nature, strong winds could easily cover the seeds with dust and soil particles.

Mature *E. victrix* fruits were collected in February 1995 at Roy Hill station. Fruits were placed in a calico bag and dried at 40°C for 12 hours. Seeds and chaff were then placed in an air tight bottle and kept at room temperature until used. *E. victrix* seed and chaff weights from random samples are given in Table 30 and Appendix 3.

Experiment I

Twelve, 10 x 10 mm bags made from nylon stocking material were used. Sets of 50 clean seeds were placed in 12 bags. Edges of bags were sealed with binding tape. On 14 February 1996 (after about 1 year of storage), 8 bags of 50 seeds were buried in an open area at 50 mm below the soil surface at Roy Hill station (lat. 22° 48' S, long. 120° 09'E). Four of these were exhumed on May 18 (94 days after burial) the other 4 were exhumed on July 5 (142 days after burial). Control bags (n = 4) were kept at room temperature at Curtin

University, Environmental Biology seed laboratory. Germination trials were conducted approximately five days after removal of the seed bags.

Unearthed seeds were observed under the light microscope prior to the germination trials. Seeds were counted out from bags and four replicates of 50 seeds were germinated on 11 cm diameter filter paper on top of 13 cm diameter filter paper. The filter papers were placed in the bottom of a large petri dish lined with sterilised and moistened vermiculate and kept in an incubation cabinet at 25°C temperature for 25 days.

Experiment II

A second experiment was set out on 9 February 1998 (after about three years of storage). Seventy four bags of 50 seeds (66 for burial + 8 for control) were prepared as before. Once again control seed bags were kept in the laboratory. The rest were divided into two groups and buried at 50 mm depth at Jackson's Bore paddock (Ethel Creek, lat. 22° 51' S, long. 120° 12'E). One group was buried under the shade of coolibah trees and the second group was buried in an open area. Sets of 4 seed bags were exhumed at 2 day intervals from 11 - 23 February 1998.

On 9 February 1998 temperature probes were carefully buried in the litter and 50 mm below the soil surface under the canopy of *E. victrix* and in an adjacent open area (Figure 62). Air temperatures were also recorded using a data logger (Datataker DT 2000) as in Chapter 5. Minimum and maximum temperatures were used for this study. Germination trials were conducted 6 days after the last batch of seed bags was exhumed (as they were exhumed at two days interval).

Table 30: Estimation of mean number of seed g^{-1} from a bulk collection of *E. victrix* from Ethel Creek station (all wt. in g).

Aliquot	Weight	Seed no.	Chaff wt	Seed wt	Seeds g^{-1}
1	0.2111	170	0.0891	0.1220	805.30
2	0.4086	249	0.2434	0.1652	611.04
3	0.2910	157	0.1945	0.0965	539.52
4	0.2457	167	0.1352	0.1105	679.69
5	0.2175	168	0.1185	0.0990	772.41
6	0.2963	259	0.1410	0.1553	874.11
7	0.2201	186	0.1022	0.1179	845.07
8	0.1981	125	0.1142	0.0839	630.99
9	0.2103	151	0.1191	0.0912	718.02
10	0.2693	233	0.1181	0.1512	865.21
Σ	2.5680	1865	1.3753	1.1927	7341.38
Mean	0.2568	186.5	0.1375	0.1193	734.14
SD	0.0638	45.0	0.0468	0.0288	116.67

Ant sampling

Pitfall traps were established to collect ant species at Roy Hill, Walkers Bore and Jackson's Bore, in coolibah woodland during April, July and October 1996. Traps were buried 10 m apart along a 110 m transect. Traps were 3 cm diameter, 15 cm long Pyrex® bottles partly filled with 50% alcohol and 50% glycerol. Traps were left in the field for three days. Ants that fell into the trap were identified against the reserve collection held in the Entomology Lab, Curtin University of Technology. After identification, all species were logged into the collection at the Entomology Lab, Curtin University. The major objective of this ant sampling was to examine any seed removing ants in the coolibah woodland. It was hypothesised that there is no seed removing ant in the coolibah woodland.

Statistical analyses

A *t*-test was used to identify any significant differences between treatments (open and shade burial) using the MINITAB 8.2 statistical program. Homogeneity of variance was checked by residual plots and germination percentage data were transformed into arcsin.

Results

Temperature (°C)

Soil temperatures recorded from Jackson's bore using the data logger showed maxima of 45 - 65°C and minima of 22 - 25°C (Figure 62). The highest maximum temperature was recorded on an open surface soil (65.3 °C) and lowest minimum was recorded in litter under shade (22.9°C). Soil temperatures of 56.2°C and 47.7°C were recorded at 50 mm depths for open and shade respectively.

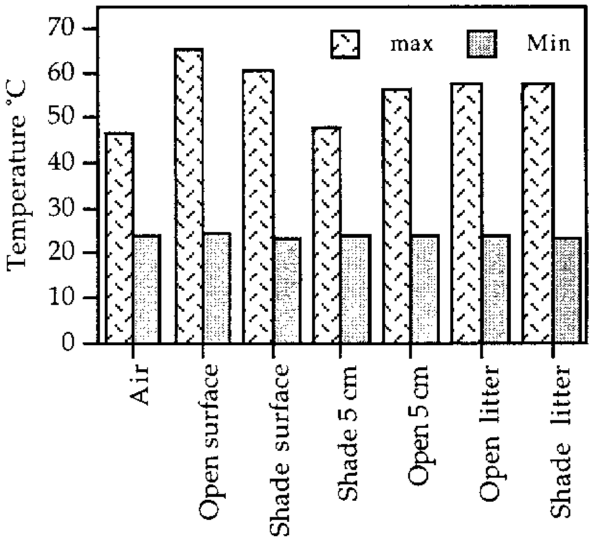

Figure 62: Maximum and minimum air and soil temperatures in the open and under shade of an *E. victrix* tree at the surface, in litter and 5 cm in soil. Temperatures were recorded for 2 weeks in the Summer of 1998 at Jackson's Bore (Ethel Creek).

Experiment I

No difference was recorded in initial and final mass of seeds. Control seed had 94% germination within 25 days (Figure 63). Increasing the duration of burial resulted in the seed viability decreasing to zero. Germination of the seeds buried for 94 days was approximately half that of the control seeds. All seeds exhumed in July 1996 (142 day after burial) were decomposed and no germination was recorded (Figure 63).

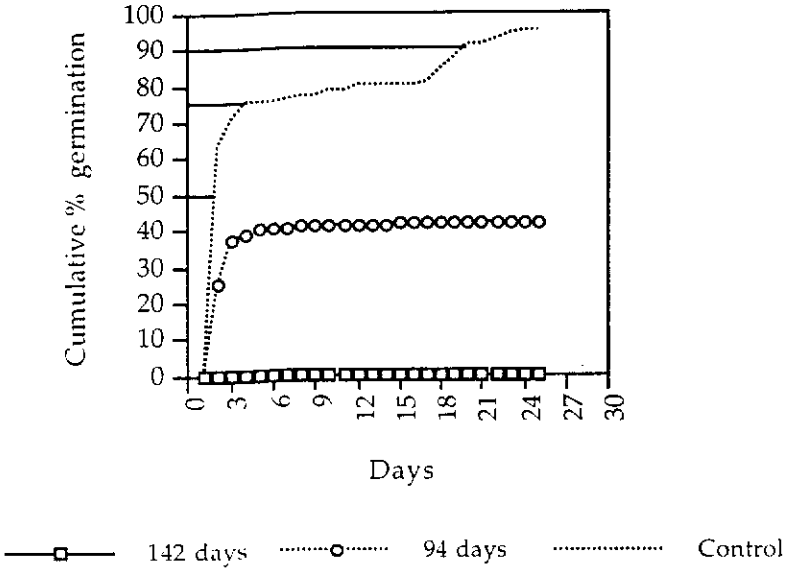

Figure 63: Germination of *E. victrix* control and burial seed sets. Arrow indicates 50% of seed germination.

Experiment II

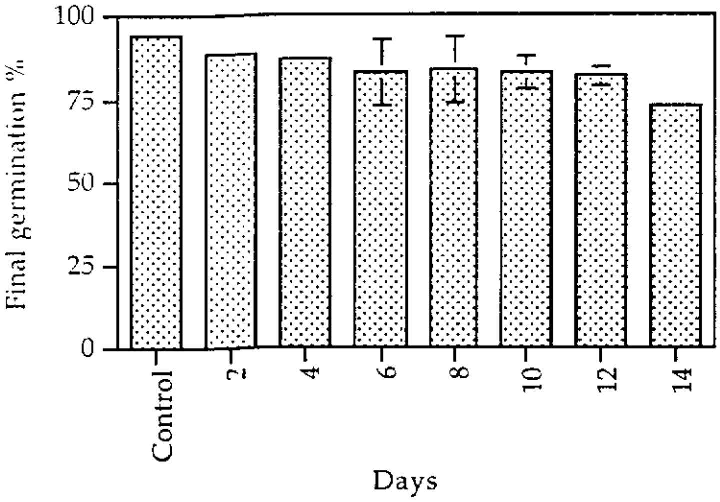

Figure 64: Final germination % (25 days from start) of *E. victrix* seed, control, 2, 4, 6, 8, 10 12 and 14 days after being exhumed in February 1998. Bars indicate standard error.

Seed buried in shade and in open sites showed no significant difference in germination ($P > 0.05$), but there is a slight reduction in percentage germination of seeds buried in an open area at 14 day after being exhumed (Figure 64, Table 31).

Table 31: Mean seed germination (± SD) for seed buried in open and shade (n = 4) (seed = 50).

Treatment	Open		Shade		t=	P =
2 Days	44.50	(± 1.91)	40.25	(± 3.40)	2.18	0.095^{NS}
4 Days	43.75	(± 2.36)	43.00	(± 4.55)	0.29	0.78^{NS}
6 Days	41.50	(± 2.08)	41.75	(± 4.79)	0.10	0.93^{NS}
8 Days	42.00	(± 1.41)	42.25	(± 3.95)	0.12	0.91^{NS}
10 Days	41.50	(± 5.26)	41.50	(± 3.42)	0.00	1.00^{NS}
12 Days	41.25	(± 2.75)	41.50	(± 1.73)	0.15	0.88^{NS}
14 Days	36.75	(± 4.03)	40.75	(± 0.50)	1.97	0.14^{NS}

NS indicates means which are not significantly different ($P > 0.05$).

Ants and seed removal

Ant pit fall traps examined over the course of 1996 showed that large numbers of ground dwelling and possibly seed removing ants such as *Pheidole ampla perthensis, Monomorium laeve* (previously identified by Yates (1995) in *Eucalyptus salmonophloia* remnant woodland, Kellerberrin, WA) were collected (Table 32). Other species such as *Iridomyrmex chasei concolor, Melophophorus* (JDM 472) and *Campanotus* spp. appear in large numbers in Coolibah woodland. In addition one particular untrapped ant species *Iridomyrmex* (JDM 597) (Sub - Family Dolichodererinae), was found only as a dweller on *E. victrix* trees. It was particularly active on the main bole and fruit capsules.

Table 32: Number of ant species collected in *E. victrix* woodland Roy Hill 1(RH1), Walkers Bore (WB) & Jackson's Bore (JB) during 1996.

	Month/Year								
	February 1996.			July 1996			October 1996		
Species	JB	RH1	WB	JB	RH1	WB	JB	RH1	WB
Calomyrmex JDM 190			1						
Camponotus JDM 598							1	1	
Camponotus sp. 1				1		1	2	9	
Camponotus JDM 310				1			1		
Camponotus JDM 290=291		1	1						
Camponotus JDM 144			3						
Iridomyrmex rufoniger suchieri Forel.		33				40			5
Iridomyrmex viridiaeneus Viehmeyer	783			2133	104		1495		14
Iridomyrmex chasei concolor Forel	5140	1281	970	5451	2189	1698	156	905	339
Iridomyrmex JDM 130					1				
Iridomyrmex JDM 595		1					10	26	5
Iridomyrmex purpureus sp		4909							
Iridomyrmex sp 1								2	
Melophorus - near- JDM 501			1						
Melophorus ANIC 1							4	18	7
Melophorus JDM 472					1	1		3	
Monomorium laeve Mayr		1		2	31	1	4	14	1
Monomorium sordidum					2				1
Monomorium disetigerum Heterick (in MS)							3		
Monomorium rothsteini Forel				1		6			4
Odontomachus ruficeps F. Smith					2		1		
Pheidole ampla perthensis Crawley		20	2		16	1		1	
Pheidole JDM 429					2				
Polyrhachis sp 1					7			1	
Rhytidoponera JDM 535						1			
Rhytidoponera violacea Forel	24	10	11	22	33	9	19	29	6
Tetramorium JDM 141					3				

Discussion

The viability of burial seed declines with time. Under experimental conditions 50% is lost by 3 months and none remain viable after 5 months burial. Boland *et al.* (1980) found that optimum germination temperature for southern Australian *Eucalyptus* species was 15 - 25°C and 30°C for northern Australian species. Similarly Bell and Bellairs (1992) reported that in *Eucalyptus oleosa*, an upland semi-arid species, optimum temperature is between 10- 20°C.

The high soil temperature at burial depth in this study suggests that seed may have been damaged, partly by high soil temperature, as laboratory sown seed retained relatively high viability. Yates (1995) reported seed coat rupture in *E. salmonophloia*, during wetting and drying cycles. In some instances *E. victrix* seed coats may have been damaged in soil.

E. victrix lacks canopy seed storage. All capsules in the current year are released by late summer. An increasing decay rate with length of time suggests seed does not survive. Synchronised mass shedding of seeds from mature *E. victrix* trees, a condition associated with natural disturbance by flood or fire plays a critical part in seedling establishment (Chapter 2). Lack of prolonged seed viability in *E. victrix* may be complemented by rapid, early establishment when optimum conditions occur. Further, long-lived species of eucalypts do not require a persistent soil seed bank as most continue seed production over many years and this ensures seeds are available for recruitment events (Kemp 1989).

There is no available evidence that ants are important seed predators of *E. victrix*. Although ants are generally more active in the summer, natural release of seed (that germinates) into moist ground probably occurs when ants may have been unhoused by flooding.

CHAPTER 9

Discussion

Introduction

This thesis represents the first attempt to describe the ecology of *E. victrix*. Little was known about the ecology of *E. victrix* prior to this study. Present populations on the floodplain of the Fortescue Valley, in the Pilbara district appear to have originated from natural seed fall coincident with optimal flooding events. The species may have slowly expanded its occupation of much of the low relief floodplain along the Fortescue River, where it now forms an unique, pristine grassy woodland. Prolonged flooding, cyclones, drought, occasional fire and strong winds are the major natural disturbances in this region where *E. victrix* has evolved to its present state. Once established, populations of saplings and trees appear resilient and well adapted to this environment.

Flooding events play a major role in the annual reproductive cycle, perhaps stimulating seed production but definitely triggering seedling establishment within the general study area (Figure 65). This species has no canopy seed storage. Observation of reproductive activity in mature trees suggests that reproduction events may be controlled by summer rain. Wet soil conditions trigger the germination of *E. victrix* seeds. As a result, large numbers of seedlings may be concealed among the luxuriant growth of seasonally recruited annuals and already established grasses. Their post-germination survival and growth depend on soil moisture and competition is intense from neighbouring trees, established grass and forb species (Figure 65).

Description of the species

During the course of this study it was observed that *E. victrix*, in favourable locations, can attain a height of 10-12 m with a single stem that is often forked once or twice. Forking tends to be lower and more pronounced on less favourable sites, or in patches of strongly competing trees when height attained may be less than 10 m (Chapter 2). Seedlings at the 4 - 6 leaf stage have stems 0.5 - 0.6 mm in thickness, saplings 35 - 46 mm whilst mature trees can attain 250 - 400 mm bole diameters 1.3 m above ground level.

The smooth, white bark of 10 - 15 mm thickness distinguishes *E. victrix* from others in the group. The wood is very hard but many trees have hollow stems. This is an impediment to the estimation of growth rings. A cross section of the mature stem reveals a large area of heart wood which is light reddish brown with a smaller area of pale yellow sap wood. Similar to many eucalypts, *E. victrix* has a swollen base to the main stem. This lignotuber is sometimes wholly or partially below the soil surface. In some trees quite a big lignotuber is completely visible above the soil surface. *E. victrix* has the capacity to produce 4 - 6 new basal shoots from the lignotuber. Mature trees contain large numbers of epicormic buds, which may sprout from the main bole and branches during recovery from severe flooding, drought or fire damage.

Mature leaves are generally 0.40 - 0.50 mm thick, lanceolate to broad lanceolate in shape. Mature leaves are generally green whilst a bluish colour is noticed on leaves of saplings. Newly flushed leaves are generally shiny and light brown in colour.

E. victrix generally flowers immediately after summer rainfall between November and February each year. Flowering appears to coincide with adequate soil moisture (e.g. after heavy rainfall and or flooding). Summer flowering may be an adaptation to the semi-arid climate, because January is usually the month when the coolibah woodland and surrounding areas receive good rainfall. The flowering period lasts for 3- 4 months. Mature fruits dry rapidly. The seeds and chaff (abortive ovules) are then shed onto moist or drying soil. Most soil and high summer temperatures create favourable conditions for fertile seeds to germinate. Seed germination is completed within 10 - 15 days. Seedlings with 4 - 6 leaves are common only after a substantial amount of rainfall (more than 250 mm), thus the seedling phase is a critical stage in the life history, similar to other *Eucalyptus* species (Chapter 2).

The root system of mature *E. victrix* consists of widely spread dense, lateral roots near the soil surface that can extend to at least 10 - 12 m from the bole. The diameters of lateral roots are of more or less uniform size for some distance from the tree. Sinker roots develop from the main lateral root and grow vertically. *E. victrix* has a long tap root system. In seedlings, the root system includes a main tap root extending from 40 to more than 400 mm in length. Their lateral roots can also spread up to 40 -50 mm in length.

Cotyledons appear as a pair of small, round leaves. These are followed by opposite pairs of juvenile leaves, the first pair developing in week old seedlings. At this stage total shoot height is 10 - 15 mm while the root is 20 - 30 mm. Shoot development is often slow in *E. victrix* seedlings. Lignotuberous basal swellings start to appear 7 - 8 weeks after germination.

Tree populations

Seedling establishment is an infrequent event in coolibah woodland. Mature tree populations appear to be very stable. Stands of trees tend to be confined to locations adjacent to the main Fortescue River channels. In grassy areas trees are fewer. Differences in height and diameter class distribution between stands in different parts of the woodland possibly reflect different past runs of wet and dry periods. Canopy shrinkage occurs and appears to be associated with the amount of rainfall received during the current year. It had been previously questioned whether this canopy shrinkage was an adaptation to environmental conditions. These studies suggest that the effects of dry conditions are overcome when major flooding or heavy rainfall events occur.

Sapling population

Establishment of *E. victrix* seedlings is strongly associated with more than average rainfall or flooding events. There is a tendency for saplings found in the edge of the gilgai to grow larger and healthier than those found inside the gilgai. Stem diameter is also bigger in saplings found at the edge of the gilgai than at other positions. The growth difference may reflect inundation of seedlings during heavy rain that may cause reduction in growth. In May 1998, 8 tagged saplings were observed flowering for the first time. This suggests that *E. victrix* attains reproductive status when saplings 2.5 m in height or 5 cm in stem diameter.

Seedling recruitment

Under control conditions 75% of *E. victrix* seeds will germinate within 4 - 5 days (Chapter 8). The seedling phase is critical to stand renewal as germinated seedlings rarely persist beyond a mean height of 10 -14 cm and the 6- 8 leaf stage. Seedlings recruited in sites disturbed by fire or flooding require greater than average rainfall during seedling establishment time. Once the seedlings are established they can survive with very low mortality rates in subsequent years. Herbivore damage to foliage occurs and it was observed that many seedlings and saplings had been grazed by insects (mainly grasshoppers e.g. *Nomadacris guttulosa, Goniaea australasiae, Happarana*? sp.). Some seedlings were damaged by livestock (Chapter 2).

Adaptation to flooding

Flooding and/or higher than average rainfall are periodic events in the coolibah woodlands. Cultivated seedlings of 1-5 month old *E. victrix* can withstand up to 8 months of inundation (Chapter 3). The implication is that in nature the species may have an advantage in that its progeny can survive such severe conditions where other species may not do so. The seedlings of *E. victrix* have morphological, physiological and anatomical adaptations (Chapter 3) that enable them to survive waterlogging. Some of these features are likely to be characteristic of adult trees although they have not yet been detected on large trees in the field. However, apparently dead trees observed on Roy Hill station after the severe drought of 1994 recovered by 1996, following major flooding in early 1995. In this case crown defoliation and top die-back of large trees may be viewed as adaptive responses to water shortage.

Comparative study on flood tolerance

E. victrix seedlings are highly tolerant of flooding as shown in Chapter 3. Flooded *E. victrix* seedlings recovered physiologically after 35 days, possibly reflecting the presence of adventitious roots. Comparisons of flood tolerance were made to examine whether waterlogging is a barrier limiting distribution of less flood-prone species to sites away from the typical floodplain area. Both *E. terminalis* and *E. leucophloia* are shown to be intolerant of waterlogging (Tang and Kozlowski 1982).

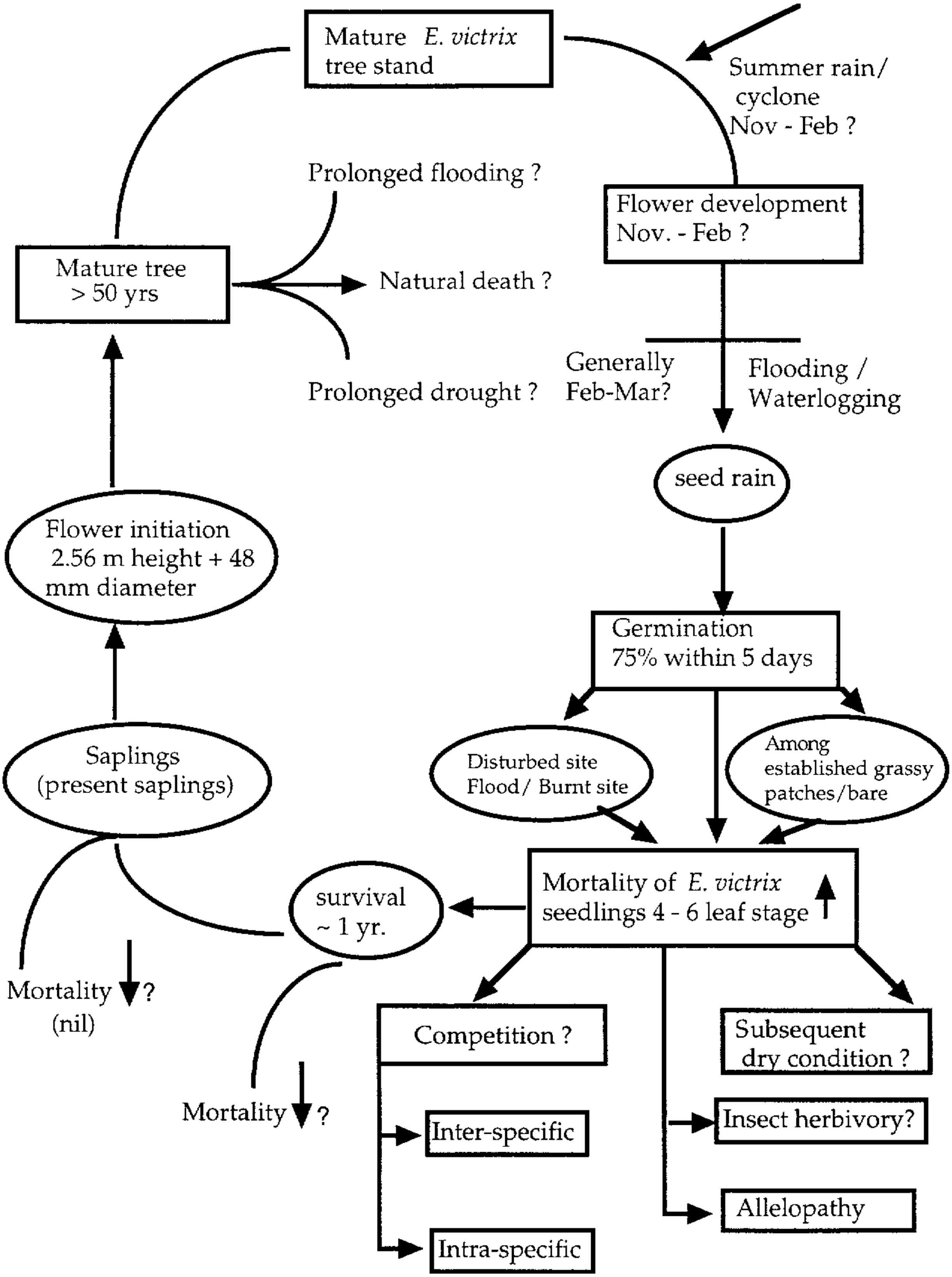

Figure 65: A proposed life cycle for the present *E. victrix* tree population found in the Fortescue Valley Pilbara.

Grass and tree association

In the coolibah woodlands examined in this study a number of both annual and perennial grasses are present in areas devoid of *E. victrix* trees (Fox *et al.* 1997 a, b, c). In many areas natural cyclical change proceeds with changing dominance of woody perennials and grasses. Individual woody plants may serve as foci for gradual grass decline (Archer *et al.* 1988). In contrast, in the Fortescue Valley, the robust annual grass *S. dielsii* thrives under the canopy of *E. victrix*. This grass can attain 1 m in favourable seasons and produce abundant seed that may remain dormant for several years. Conditions under *E. victrix* trees appear to provide optimal conditions for this species, and possibly others (Chapter 5). As the trees age it appears that nutrients become more concentrated under the canopy. This is a function of localised bark and fine litter accumulation and the trees possibly acting as nutrient pumps, drawing nutrients from deep horizons and also from beyond the canopy zone (Kellmann 1979, Scholes 1990).

Grazing is an important factor in the conversion of grasslands to what livestock managers consider to be less desirable shrublands (Milchunas and Lauenroth 1993). In the WA rangelands a number of woody species are considered to be increasers in grazed communities (Mitchell and Wilcox 1994). Tree growth into former grass patches is often slow but persistent, with the chance of establishment enhanced by disturbance (Crow *et al.* 1994). Increases of dominant species under grazing are predicted by Milchunas and Lauenroth (1993) under some conditions. However, decreases are more likely among bunch grasses than other life-forms and more likely among perennials than annuals. In the absence of cattle, *Eragrostis intermedia* is a dominant perennial grass in semi-arid US grasslands but its long-term abundance appears to depend on episodic renewal, particularly during periods of reduced precipitation (Bock *et al.* 1995).

In the present study, the sub-shrub *Malvastrum americanum* was common under the canopy of *E. victrix* with *S. dielsii* absent, but not elsewhere. This suggests that in these woodlands particular species may come to locally dominate the favourable mesic conditions that occur under the canopy and that once a particular species has established others may be deterred by the competitive effect of the local dominant.

Competition

Glasshouse experiments demonstrated that density of neighbouring grass species and time of establishment influence growth (height, photosynthetic area, root and shoot dry mass) of *E. victrix* seedlings. Photosynthetic area is vital to make the most beneficial use of the resources available (Ritchie 1974). Thus high summer mortality in the field is likely to be greater with competition from established grasses.

Inter-specific competition is more intense than intra-specific competition. Field studies revealed that considerable numbers of seedlings died during the establishment phase. However, natural disturbance such as fire and flooding create suitable conditions for *E. victrix* seedlings to establish in the woodland, evidenced by events in the past several years. Heavy seed production contributes to mass seedling establishment. Poor seed viability (Chapter 8) is another factor that needs to be considered. Later seedling emergence results in high mortality and poor growth.

Allelopathy

Lack of ground cover or failure of ground cover species to establish beneath the canopy of some isolated *E. victrix* trees, was hypothesised as at least partly attributable to allelopathic effects (Chapter 7). Allelopathic responses have been shown in some *Eucalyptus* woodlands. Del Moral and Muller (1970) described the allelopathic effects of river red gum on ground cover species, in California-plantations. Suppression may be attributable to phenolic acids and terpenes that leach from leaves or bark. Litter accumulation beneath the canopy may also hinder the germination of ground cover species.

A preliminary biossay with *L. sativa* seed demonstrated that *E. victrix* leaf and bark tissues possess toxic allelopathic substances. Leaf extract is more potent in affecting germination and radicle growth of *L. sativa* than bark extract or leaf leachate.

Inhibitory effects of *E. victrix* leaf leachate were demonstrated on seedlings of three eucalypts and three grass species. *E. victrix* seedling shoot and root biomass was significantly reduced by its own leaf leachate. Seedling recruitment of *E. victrix* beneath the canopy may be affected by allelopathic substances. However, as normal seedling recruitment events occur only after more than average rainfall or flooding events, concentrations of toxic phenolic substances may be reduced. Materials may be leached of allelopathic substances to lower horizons of the soil (Del Moral and Muller 1970).

No biomass reduction was observed in *E. leucophloia*, but leachate had an impact on *E. microtheca* shoot and root biomass. Of the grasses tested, it is interesting to note that *S. dielsii* root biomass was not affected by the leachate.

High Performance Liquid Chromatography (HPLC) revealed that fresh leaf and bark contain eleven and eight possible allelopathic substances respectively. *E. victrix* fresh leaf material contains water soluble phytochemicals which are capable of reducing the growth of tested grass species typical of the coolibah woodland.

Seed longevity

Seed longevity plays a major role in most plant communities especially where plants experience severe drought and are particularly dependent on rainfall or flooding. Recruitment of seedlings after summer rain or flooding events, involves the current years seed rather than that from previous years. Fallen seeds may be damaged or eaten by predators. Viability of seed is reduced from 14 days burial and is severe after 94 days of burial (Chapter 8). All viability is lost after 142 days, confirming that seedling recruitment is from recently produced seed.

Future Studies

Further research is needed under a number of headings

- Growth of *E. victrix* seedlings under different drought regimes.
- Seasonal variation of water usage of seedling, sapling and tree populations.
- Further exploration of the relationship between micro-topography and growth of *E. victrix* .
- Leaf and flower production in relation to rainfall.
- Natural disturbance (flooding and fire) and its effect on seedling recruitment and subsequent mortality and growth.
- Prolonged flooding effects and recovery (post-flooding performance) of *E. victrix* .
- Nutrient cycling in *E. victrix* woodland.
- Effect of insect herbivory on growth of trees.
- Distribution of *E. victrix* in relation to flood flow.

In conclusion, the present study was a multi-disciplinary approach to investigate the ecology of *E. victrix*. The research presented in this thesis has contributed to an understanding of the ecology of *E. victrix* found on the floodplain of the Fortescue Valley in the Pilbara district of WA and I believe a useful foundation has been laid for future research work.

References

Abbott, I. & Loneragan, O. (1986). Ecology of Jarrah (*Eucalyptus marginata*) in the northern jarrah forest of Western Australia. Bulletin No: 1. Department of Conservation and Land Management, Perth. Western Australia.

Abeles, F. B. (1973). **Ethylene in Plant Biology**. Academic Press, New York. pp. 302

Adkins, S. W. & Sowerby, M. S. (1996). Allelopathic potential of the weed, *Parthenium hysterophorus* L., in Australia. *Plant Protection Quarterly* **11:** 20 - 23.

Ahmed, A. El H. (1977). The silviculture and management of *Eucalyptus microtheca* irrigated plantations in the Gezira of the Sudan. Forest Research Institute (Soba) *Bulletin No.* **1** pp. 64.

Ahmed, N., Hussain, F. & Akram, M. (1984). The allelopathic potential of *Eucalyptus tereticornis* Sm. *Pakistan Journal of Science and Industrial Research* **27:** 88 - 91.

Al-Mousawi, A. H. & Al-Naib, F. A. G. (1975). Allelopathic effects of *Eucalyptus microtheca*. *Journal of University Kuwait* (*Science.*) **2:** 59 - 65.

Al-Mousawi, A. H. & Al-Naib, F. A. G. (1976). Volatile growth inhibitors produced by *Eucalyptus microtheca*. *Bulletin Iraqui Biological Research Center* **7:** 17 - 23.

Al-Naib, F. A. G. & Al-Mousawi, A. H. (1976). Allelopathic effects of *Eucalyptus microtheca*. Identification and characterisation of the phenolic compounds in *Eucalyptus microtheca*. *Journal of University Kuwait* (*Science.*) **3:** 83-87.

Anderson, D. J. (1967). Studies on structure in plant communities. Part V. Pattern in *Atriplex vesicaria* communities in south-eastern Australia. *Journal of Ecology* **15:** 451 - 458.

Angeles, G., Evert, R. F. & Kozlowski, T. T. (1986). Development of lenticels and adventitious roots in flooded *Ulmus americana* seedlings. *Canadian Journal of Forest Research* **16:** 585 - 590.

Anon (1989) Colour chart- Royal Horticultural Society (RHS). London.

Antonovics, J. & Levin, D. A. (1980). The ecological and genetic consequence of density-dependent regulation in plants. *Annual Review of Ecology and Systematics* **11:** 411-452.

Anwar, C. (1991). The effects of *Eucalyptus* allelopathy on the growth of *Shorea palembanica* seedlings. *Bulletin Penelitian Hutan* **545:** 1 - 10.

Archer, S., Scifres, C., Bassham, C. R. & Maggio, R. (1988). Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* **58**, 111-127.

Arnold, J. F. (1964). Zonation of the understorey vegetation around a juniper tree. *Journal of Range Management* **17:** 41 - 42.

Ashton, D. H. (1979). Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Victoria. *Australian Journal of Ecology* **4:** 265 - 277.

Ashton, D. H. & Chappill, J. A. (1989). Secondary succession in post-fire scrub dominated by *Acacia verticillata* (L'Herit.) Willd. at Wilsons Promontory, Victoria. *Australian Journal of Botany* **37:** 1 - 18.

Atkins, K. J. (1985). Studies into the ecological revegetation of an iron ore mine site in the arid Pilbara region of Western Australia. Ph. D. Thesis. University of Western Australia.

Barry Gratte (1997). Station Manager, Ethel Creek, Pilbara, WA.

Battaglia, M. & Reid, J. B. (1993). The effect of microsite variation on seed germination and seedling survival of *Eucalyptus delegatensis*. *Australian Journal of Botany* **41:** 169 - 181.

Battaglia, M. & Wilson, L. P. (1990). Effect of shelter woods on stocking and growth of regeneration in dry high altitude *Eucalyptus delegatensis* forests. *Australian Forestry* **53:** 259 - 265.

Beard, J. S. (1975). Vegetation Survey of Western Australia: Pilbara. University of Western Australia Press. Western Australia. pp. 120

Bell, D. T. & Bellairs, S. M. (1992). Effects of temperature on the germination of selected Australian native species used in rehabilitation of bauxite mining disturbance in Western Australia. *Seed Science and Technology* **20:** 47 - 55.

Bell, D. T., McComb. J. A., van der Moezel, P. G., Bennett, I. J. & Kabay, E. D. (1994). Comparisons of selected and cloned plantlets against unselected seedlings for rehabilitation of waterlogged and saline discharge zones in Australian agricultural catchments. *Australian Forestry* **57** : 21 - 27.

Bell, D. T. & Williams, J. E. (1997). Eucalypt eco-physiology. pp 168 - 196. *In* Williams, J. & Woinarski, J. (eds). Cambridge University Press. United Kingdom. 430 pp.

Belsky, A. J., Amundson, R. G., Duxbury, J. M., Riha, S. J., Ali, A. R. & Mwonga, S. M. (1989). The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* **26**: 1005 - 1024.

Bentham, G. (1867). Flora Australiensis Vol. 3. L. Reeve & Co., London.

Bignell, C. M., Dunlop, P. J., Brophy, J. J. & Jackson, J. F. (1994). Volatile leaf oils of some South-Western and Southern Australian species of the Genus *Eucalyptus*. Part I: Subgenus *Symphyomyrtus*, Section Dumaria, Series Incrassatae. *Flavour and Fragrance Journal* **9:** 113 - 117.

Blair, G. J., Chinoim, N., Lefroy, R. D. B., Anderson, G. C. & Crocker, G. J. (1991). Australian soil sulfur test for pastures and crops. *Australian Journal of Soil Research* **29**: 619- 626.

Blake, S. T. (1953). Botanical contributions of the northern Australia regional survey - I. Studies on northern Australian species of *Eucalyptus*. *Australian Journal of Botany* **1:** 185 - 352.

Blakely, W. F. (1965). **A Key to the *Eucalyptus*.** 3rd edition. Forestry and Timber Bureau, Canberra. pp. 359.

Bock C. E., Bock, J. H., Grant, M. C. & Seastedt T. R. (1995). Effects of fire on abundance of *Eragrostis intermedia* in a semi-arid grassland in southeastern Arizona. *Journal of Vegetation Science* **6**, 325-328.

Boland, D. J., Brooker, M. I. H. & Turnbull, J. W. (1980). **Eucalyptus Seed.** CSIRO: Melbourne. pp. 191.

Bosch, O. J. H. & van Wyk, J. J. P. (1970). The influence of bushveld trees on the productivity of *Panicum maximum*. *Proceedings of the Grasslands Society of South Africa* **5**: 69 - 74.

Bowman, D. M. J. S & Kirkpatrick, J. B. (1986). Establishment, suppression and growth of *Eucalyptus delegatensis* R. T. Baker in multi-aged forests. III. Interspecific allelopathy, competition between adult and juveniles for moisture and nutrients, and frost damage to seedlings. *Australian Journal of Botany* **34:** 81 - 94.

Bren, L. J. (1988). Flooding characteristics of a riparian red gum forest. *Australian Forestry* **51:** 57 - 62.

Brooker, M. I. H. & Kleinig, D. A. (1994). **Field Guide to Eucalyptus**: Northern Australia. Inkata Press, Sydney. pp. 383.

Bryant, W. G. (1971). Grazing, burning and regeneration of tree seedlings in *Eucalyptus pauciflora* woodlands. *Journal of Soil Conservation New South Wales* **25:** 121 - 134.

Burrows, N., Gardiner, G., Ward, B. & Robinson, A. (1990). Regeneration of *Eucalyptus wandoo* following fire. *Australian Forestry* **53:** 248 - 258.

Burrows, W. H. (1974). Trees and shrubs in mulga lands. *Queensland Agricultural Journal* **100:** 322 - 329.

Bush, J. K. & Van Auken, O. W. (1990). Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. *Botanical Gazette* **151:** 234 - 239.

Caldwell, J. M., Sucoff, E. I. & Dixon. R. K. (1995). Grass interference limits resources availability and reduces growth of juvenile red pine in the field. *New Forests* **10:** 1 - 15.

Callaway, R. M., Nadkarni, N. M. & Mahall, B. E. (1991). Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* **72**: 1484 - 1499.

Campbell, B. M., Frost, P., King, J., Mawanza, M. & Mhlanga, L. (1993). The influence of trees on soil fertility and microbial activity, Matobo, Zimbabwe. pp. 197-208. *In* Piearce, G. D. & Gumbo, D. J. (eds.). **The Ecological Management of Indigenous Forests in Southern Africa**. Zimbabwe Forestry Commission, Harare.

Charley, J. L. & West, N. E. (1975). Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology* **63**: 945-963.

Clemens, J. & Pearson, C. J. (1977). The effect of water-logging on the growth and ethylene content of *Eucalyptus robusta* Sm. (swamp mahogany). *Oecologia* **29:** 249 - 255.

Clemens, J., Kirk, A. M. & Mills, P. D. (1978). The resistance to waterlogging of three *Eucalyptus* species- the effect of waterlogging and an ethylene-releasing substance on *E. robusta, E. grandis* and *E. saligna*. *Oecologia* **34:** 125 - 131.

Crow T R., Johnson W C. & Adkisson C S. (1994). Fire and recruitment of *Quercus* in a post agricultural field. *American Midland Naturalist* **131,** 84-97.

Cunningham, T. M. (1960). The natural regeneration of *Eucalyptus regnans*. School of Forestry, University of Melbourne, Bulletin No. **1:** 158 pp.

Danielsen, K. C. & Halvorson, W. L. (1991). Valley oak seedling growth associated with selected grass species. USAID Forest Service General *Technical Report* pp 126.

Davidson, N. J. & Reid, J. B. (1985). Frost as a factor influencing the growth and distribution of subalpine *Eucalyptus*. *Australian Journal of Botany* **33:** 657 - 667.

Davidson, N. J. & Reid, J. B. (1987). The influence of hardening and waterlogging on the frost resistance of subalpine eucalypts. *Australian Journal of Botany* **35:** 91 - 101.

Davison, E. M. & Tay, F. C. S. (1985). The effect of waterlogging on seedlings of *Eucalyptus marginata*. *New Phytologist* **101:** 743 - 753.

Day, R. W. & Quinn, G. P. (1989). Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**: 133 - 138.

Deevey, E. S. (1947). Life tables for natural populations of animals. *Quarterly Review of Biology* **22:** 285 - 314.

del Moral, R. & Muller, C. H. (1970) The allelopathic effects of *Eucalyptus camadulensis*. *The American Midland Naturalist* **83:** 254 - 282.

del Moral, R., Willis, R. J. & Ashton, D. H. (1978). Suppression of coastal heath vegetation by *Eucalyptus baxteri*. *Australian Journal of Botany* **26:** 203 - 219.

Denny, F. E. & Miller, L. P. (1935). Production of ethylene by plant tissue as indicated by the epinasty response of leaves. *Contribution of Boyce Thompson Institute* **7:** 97 - 102.

Dexter, B. D., Rose, H. J. & Davies, N. (1986). River regulation and associated forest management problems in the River Murray red gum forest. *Australian Forestry* **49:** 16 - 27.

Dietz, H. & Winterhalter, P. (1996). Phytotoxic constituents from *Bunias orientalis* leaves. *Phytochemistry* **42:** 1005 -1010.

Dionigi, C. P., Mendelssohn, I. A. & Sullivan, V. I. (1985). Effects of soil waterlogging on the energy status and distribution of *Salix nigra* and *S. exigua* (Salicaceae) in the Atchafalaya River basin of Louisiana. *American Journal of Botany* **75:** 109 - 119.

Distel, R. A., Peláez, D. V., Boo, R. M., Mayor, M. D. & Elía, O. R. (1996). Growth of *Prosopis caldenia* seedlings in the field as related to grazing history of the site and in a greenhouse as related to different levels of competition from *Stipa tenuis*. *Journal of Arid Environments* **32:** 251 - 257.

Doran, J. C. & Boland, D. J. (1984). Effects of temperature on germination of *Eucalyptus microtheca*. *Australian Forest Research* **14**: 49-55.

Ehleringer, J. R. (1984). Intra specific competition effects on water relations, growth and reproduction in *Eucelia farinose*. *Oecologia* **63:** 153 - 158.

Enright, N. J. & Lamont, B. B. (1989). Seed banks, fire seasons, safe sites and seedling recruitment in five co-occurring *Banksia* species. *Journal of Ecology* **77:** 1111 - 1122.

Evenari, M. & Newman, G. (1952). The germination of lettuce seeds. ll. The influence of fruit coat, seed coat and endosperm upon germination. *Bulletin of Research Council of Israel* **2:** 75 - 78.

Ferguson, D. E. (1991). Allelopathic potential of western coneflower (*Rudbeckia occidentalis*). *Canadian Journal of Botany* **69:** 2806 - 2808.

Fireman, M. & Hayward, H. E. (1952). Indicator significance of some shrubs in the Escalante Desert, Utah. *Botanical Gazette* **114:** 143 - 155.

Fisher, F. M., Zack, J. C., Cunningham, G. L. & Whitford, W. D. (1988). Water and nitrogen effects on the growth and allocation patterns of creosote bush in the northern Chihuahuan Desert. *Journal of Rangeland Management* **41:** 387 - 391.

Foster, M. A., Scifres, C. J. & Jacoby, P. W. (1984). Herbaceous vegetation-lotebush [*Ziziphus obtusifolia* (T. & G.) Gray var. *obtusifolia*] interactions in north Texas. *Journal of Range Management* **37**: 317- 320.

Fox, J. E. D. & O' Connell, K. A. (1994). Changes in coolibah populations and ground cover vegetation due to seasonal effects downstream of Ophthalmia Dam. *Report Commissioned by BHP Iron Ore*. pp 129.

Fox, J. E. D (1996). Status and trends in floodplain vegetation of the Fortescue Valley 1991 - 1995. *Report Commissioned by BHP Iron Ore*. pp 73.

Fox, J. E. D. & Jeanes, B. H. (1996). Seasonal changes to herbage in floodplain vegetation and annual woody growth. *Report Commissioned by BHP Iron Ore*. pp 154.

Fox, J. E. D. & Wilcox, D. G. (1992). Assessment of impacts on vegetation downstream of Ophthalmia Dam. *Report to BHP Iron Ore*. pp 96.

Fox, J. E. D., Bainbridge, S. & Coulson, D. S. (1997a). Vegetation condition downstream of Ophthalmia Dam in the floodplain of the Fortescue Valley. *Report Commissioned by BHP Iron Ore*. pp 194.

Fox, J. E. D., Bainbridge, S. & Coulson, D. S. (1997b). Grass species management in the floodplain of the Fortescue Valley. Report to BHP Iron Ore. 20. 08. 1997.

Fox, J. E. D., Bainbridge, S. & Coulson, D. S. (1997c). Vegetation condition downstream of Ophthalmia dam in the Floodplain of the Fortescue valley. *A Report Commissioned by BHP Iron Ore*.pp -194.

Gilbert, J. M. (1961). The effect of browsing by native animals on the establishment of seedlings of *Eucalyptus regnans* in the Florentine Valley, Tasmania. *Australian Forestry* **25:** 116 - 121.

Gill, A. M. (1981). Adaptive responses of Australian vascular plant species to fires. *In* **Fire and the Australian Biota** (Eds A. M. Gill, R. H. Groves & I. R. Noble) pp 243 - 272. Australian Academy of Science: Canberra.

Gomes, S. A. R. & Kozlowski, T. T. (1980a). Growth response and adaptation of *Fraxinus pennsylvanica* seedlings to flooding. *Plant Physiology* **66:** 267 - 271.

Gomes, S. A. R. & Kozlowski T. T. (1980b). Effect of flooding on *Eucalyptus camaldulensis* and *Eucalyptus globulus* seedlings. *Oecologia* **46:** 139 - 142.

Goor, A. Y. & Barney, C. W. (1968). **Forest Tree Planting in Arid Zones.** Ronald Press, New York. pp. 409.

Gordon, D. R., Walker, J. M., Menke, J. W. Rice, K. J. (1989). Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia* **79:** 533 - 541.

Graham, R. (1998). The ecology of some annual grass species of the Fortescue floodplain, Pilbara, Western Australia. Honours thesis, Curtin University, Western Australia. pp. 100.

Grant, C. D. & Bell, D. T. (1994). Implications of seedling emergence to bauxite mining restoration Western Australia. In *Proceedings of the 9th Annual Environmental Workshop* pp. 103- 126. (Australian Mining Industry Council: Karratha.)

Green, J. W. (1985). **Census of the Vascular Plants of Western Australia**. Second Edition. Western Australian Herbarium, Perth. pp - 311.

Grice, A. C., Westoby, M. & Torpy, C. (1994). Dynamics and population structure of *Acacia victoriae* Benth. *Australian Journal of Ecology* **19:** 10 - 16.

Gutierrez, J. R., Meserve, P. L. Contreras, L. C., Vasquez, H. & Jaksic, H. (1993). Spatial distribution of soil nutrients and ephemeral plants underneath and out-side the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia* **93:** 347 - 352.

Harper, J. L. (1977). **Population Biology of Plants.** Academic Press London. pp. 892.

Haworth, K. & McPherson, G. R. (1994). Effects of *Quercus emoryi* on herbaceous vegetation in a semi-arid savanna. *Vegetatio* **112:** 153 - 159.

Heisey, R. M. & Delwiche, C. C. (1985). Allelopathic effects of *Trichostema lanceolatum* (Labiatae) in the California annual grassland. *Journal of Ecology* **73:** 729 - 742.

Hill, K. D. & Johnson, L. A. S. (1994). Systematic studies in eucalyptus 6. A revision of the coolibah, *Eucalyptus* subgenus Symphyomyrtus section Adnataria series Oliganthae sub series Microthecosae (Myrtaceae). *Telopea* **5:** 743 -771.

Hill, W. E. & Isoi, K. (1965). Variation in the chemical composition of *Eucalyptus sideroxylon*. *Phytochemistry* **4:** 541 - 550.

Hook, D. D. (1984). Adaptations to flooding with fresh water. pp 265 - 294. *In* Kozlowski, T. T. (ed). **Flooding and Plant Growth**. Academic Press, New York.

Hsiao, T. C. & Acevedo, E. (1974). Plant responses to water deficits water use efficiency and drought tolerance. *Agriculture and Forest Meteorology* **14:** 59 - 84.

Hughes, F. M. R. (1988). The ecology of African floodplain forests in semi-arid and arid zones. *Journal of Biogeography* **15:** 127 - 140.

Hughes, F. M. R. (1990). The influence of flooding regimes on forest distribution and composition in the Tana river floodplain, Kenya. *Journal of Applied Ecology* **27:** 475 - 491.

Huiquan, Bi, & Turvey, N. D. (1994). Intra-specific competition between seedlings of *Pinus radiata, Eucalyptus regnans* and *Acacia melanoxylon*. *Australian Journal of Botany* **42:** 61 - 70.

Hytönen, J. (1992). Allelopathic potential of peatland plant species on germination and early seedling growth of scots pine, silver birch and downy birch. *Silva Fennica* **2:** 63 - 73.

Isbell, R. A. F. (1996). The Australian Soil Classification. CSIRO, Australia pp. 143.

Jackson, E. L. & Roy, J. (1986). Growth patterns of Mediterranean annual and perennial grasses under simulated rainfall regimes of Southern France and California. *Oecologia Plantarum* **7:** 191 - 212.

Johnson, L. A. S. & Hill, K. D. (1994). New taxa and combinations in *Eucalyptus* and *Angophora* (Myrtaceae). *Telopea* **4:** 37- 108.

Johnston, R. D. & Marryatt, R. (1965). Taxonomy and nomenclature of eucalypts. Forestry and Timber Bureau, Canberra, Leaflet No. 92. pp. 23

Kawase, M. (1974). Role of ethylene in induction of flooding damage in sunflower. *Physiology of Plants* **31:** 29 - 38.

Kellman, M. (1979). Soil enrichment by neotropical savanna trees. *Journal of Ecology* **67:** 565 - 577.

Kemp, P. R. (1989). Seed banks and vegetation and process in deserts. pp- 257 - 281. *In* Leck, A. Parker, V. T. & Simpson, R. L. (eds) **Ecology of Soil Seed Banks**. Academic press Inc. California.

Kennard, D. G. & Walker, B. H. (1973). Relationships between tree canopy cover and *Panicum maximum* in the vicinity of Fort Victoria. *Rhodesian Journal of Agricultural Research* **11:** 145-153.

Kile, G. A. (1974). Insect defoliation in the eucalypt regrowth forests of southern Tasmania. *Australian Forest Research* **6:** 9 - 18.

Kohli, R. K., Chaudhry, P. & Kumari, A. (1988a). Impact of *Eucalyptus* on *Parthenium* - a weed. *Indian Journal of Rangeland Management* **9:** 63 - 67.

Kohli, R. K., Karu, K. & Kumari, A. (1988b). Inhibition of seed germination of *Vigna umbellata* in response to *Eucalyptus globulus* Labill. Allelochemicals. Proceedings of the International Congress of Plant Physiology, New Delhi. pp. 1292 - 1296.

Kohli, R. K. & Singh, D. (1991). Allelopathic impact of volatile components from *Eucalyptus* on crop plants. *Biologia Plantarum* **33:** 475 - 483.

Kozlowski, T. T. (1982). Water supply and tree growth Part II. Flooding *Forestry Abstracts* **43:** 145 - 161.

Kozlowski, T. T. (1984a). Plant responses to flooding of soil. *Bioscience* **34:** 162 - 167.

Kozlowski, T. T. (1984b). Responses of woody plants to flooding. pp. 129 - 164. *In* Kozlowski, T. T. (ed). **Flooding and Plant Growth.** Academic Press, New York. pp. 356.

Kozlowski, T. T., Kramer, P. J. & Pallardy, S. G. (1991). **The Physiological Ecology of Woody Plants**. Academic Press, New York. pp. 657.

Kramer, P. J. (1969). **Plant and Soil Water Relationships: A Modern Synthesis.** McGraw-Hill New York. pp. 482.

Kummerow, J., Ellis, B. A. & Mills, J. N. (1985). Post-fire seedling establishment of *Adenostoma fasciculatum* and *Ceanothus greggii* in southern California chaparral. *Madrono* **32:** 148 - 157

Ladiges, P. Y. & Kelso. A. (1977). The comparative effects of waterlogging on two populations of *Eucalyptus viminalis* Labill. and one population of *E. ovata* Labill. *Australian Journal of Botany* **25:** 159 - 169.

Lamont, B. B. (1985). Gradient and zonal analysis of understorey suppression by *Eucalyptus wandoo*. *Vegetatio* **63:** 49 - 66.

Lange, R. T. & Reynolds, T. (1981). Halo effects on native vegetation. *Transactions of the Royal Society of South Australia* **105:** 213 -214.

Leigh, J. H. & Holgate, M. D. (1979). The responses of the understorey of forests and woodlands of the Southern Tablelands to grazing and burning. *Australian Journal of Ecology* **4:** 25 - 45.

Lisanework, N. & Michelsen, A. (1993). Allelopathy in agroforestry systems: The effects of leaf extracts of *Cupressus lusitanica* and three *Eucalyptus* spp. on four Ethiopian crops. *Agroforestry Systems* **21:** 63 - 74.

Loneragan, O. W & Loneragan, J. F. (1964). Ashbed and nutrients in the growth of seedlings of karri (*Eucalyptus diversicolor* F.v.M.). *Journal of Royal Society of Western Australia* **47:** 75 - 80.

Lunt, I. D. (1995). Seed longevity of six native forbs in a closed *Themeda triandra* Grassland. *Australian Journal of Botany* **43:** 439 - 449.

Macias, F, A., Torres, A., Molinillo, M. G. J., Varela, M. R. & Castellano, D. (1996). Potential allelopathic sesquiterpene lactones from sunflower leaves. *Phytochemistry* **43:** 1205 - 1215.

Mack, R. N. & Harper, J. L. (1977). Interference in dune annuals: spatial pattern and neighbourhood effects. *Journal of Ecology* **65:** 345 - 363.

Maiden, J. H. (1903 - 33). **A Critical Revision of the Genus Eucalyptus**. Government Printer, Sydney.

May, F. E. & Ash, J. E. (1990). An assessment of the allelopathic potential of *Eucalyptus*. *Australian Journal of Botany* **38:** 245 - 254.

McComb. J. A., Bennett, I. J., van der Moezel, P. G. & Bell, D. T. (1989). Biotechnology enhances utilisation of Australian woody species for pulp, fuel and land rehabilitation. *Australian Journal of Biotechnology* **3:** 297 - 301.

McPherson, G. R., Rasmussen, G. A., Webster, D. B. & Masters, R. A. (1991). Vegetation and soil zonation associated with *Juniper pinchotti* Sudw. trees. *Great Basin Naturalist* **51**: 316 - 324.

Megonigal, J. P. & Day, F. P. (1992). Effects of flooding on root and shoot production of bald cypress in large experimental enclosures. *Ecology* **73**: 1182-1193.

Milchunas, D. G. & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**, 327-366.

Mills, J. N. (1983). Herbivory and seedling establishment in post-fire southern California chaparral. *Oecologia* **60:** 267 - 270.

Mitchell, A. A. & Wilcox, D. G. (1994). **Arid Shrubland Plants of Western Australia**. University of WA Press, Perth, Western Australia. pp. 478.

Mitchell. A. A. (1998). Agricultural Adviser, Department of Agriculture, Perth, WA.

Moore, R. M. & Williams, J. D. (1976). A study of a subalpine woodland-grassland boundary. *Australian Journal of Ecology* **1:** 145 - 153.

Moyo, C. S. & Campbell, B. M. (1996). Grass species composition under and outside tree canopies in a semi-arid savanna rangeland in Zimbabwe. pp. 194-200. *In* Mushove, P. T., Shumba, E. M. & Matose, F. (eds.). **Sustainable Management of Indigenous Forests in the Dry Tropics**. Zimbabwe Forestry Commission, Harare.

Newsome, R. E., Kozlowski, T. T. & Tang, Z. C. (1982). Responses of *Ulmus americana* seedlings to flooding of soil. *Canadian Journal of Botany* **60:** 1668 - 1685.

Ng, R. Y. H., Waugh, A. S., Cicero, C., Pearce, L. & Tan, B. (1991). Assessment of the hydrological impact of Ophthalmia Dam, Water Authority of Western Australia. Report No **WS 80**.

Nishimura, H., Kaku, K. & Nakamura, T., Fukawaza, V. & Mizutani. J. (1982). Allelopathic substances, (±)-p-menthene - 3, 8 diols isolated from *Eucalyptus citriodora*. Hook. *Agricultural and Biological Chemistry* **46:** 319 - 320.

Noble, I. R. (1984). Mortality of lignotuberous seedlings of *Eucalyptus* species after an intense fore in montane forest. *Australian Journal of Ecology* **9:** 47 - 50.

Noble, I. R. (1989). Ecological traits of the eucalypts L'Herit. Subgenera *Monocalyptus* and *Symphyomyrtus*. *Australian Journal of Botany* **37:** 207 - 224.

O'Dowd, D. J. & Gill, A. M. (1984). Predator satiation and site alteration following fire: mass reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. *Ecology* **65:** 1052 - 1066.

Parker, V. T. & Kelly, V. R. (1989). Seed banks in California Chaparral and other Mediterranean climate shrub lands. pp 231 - 255. *In* Leck, A. Parker, V. T. & Simpson, R. L. (eds) **Ecology of Soil Seed Banks**. Academic press Inc. California.

Parker, V. T. & Muller, C. H. (1982). Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *American Midland Naturalist* **107:** 69 - 81.

Parsons, M., Bren, L. J. & Dexter, B. D. (1991). Riverine forests of the central Murray valley. pp.. 271- 283. *In* McKinnell, F. H., Hopkins, E. R. & Fox, J. E. D. (eds). **Forest Management in Australia.** Surrey Beatty & Sons Pty Ltd, Chipping Norton, NSW, Australia.

Paulsen, H. A. (1953). A comparison of surface soil properties under mesquite and perennial grass. *Ecology* **34:** 727 - 732.

Payne, A. L. & Mitchell, A. A. (1992). An assessment of the impact of Ophthalmia Dam on the floodplain of the Fortescue River On Ethel Creek and Roy Hill Stations. WA Department of Agriculture, *Technical Report* **124**. pp 69.

Pellissier, F. (1994). Effect of phenolic compounds in humus on the natural regeneration of spruce. *Phytochemistry* **36:** 865 - 867.

Putnam, A. R. & Tang, C. H. (1986). **The Science of Allelopathy**. John Wiley and Sons, New York. pp. 317.

Ranney, T. G. & Bir, R. E. (1994). Comparative flood tolerance of birch root stocks. *Journal of American Society of Horticultural Science* **119:** 43 - 48.

Rao, N. S. & Reddy, P. C. (1984). Studies of the inhibitory effects of *Eucalyptus* (hybrid) leaf extracts on the germination of certain food crops. *Indian Forester* **110:** 218 - 222.

Regehr, D. L., Bazzaz, F. A. & Boggess, W. A. (1975). Photosynthesis, transpiration, and leaf conductance of *Populus deltoides* in relation to flooding and drought. *Photosynthetica* **9:** 52 - 61.

Rice, E. L. (1974). **Allelopathy**. 2nd Edition. Academic Press, New York. London. pp. 353.

Ritchie, G. A. (1974). Atmospheric and soil water influences on the plant water balance. *Agricultural Forest Meteorology* **14:** 183 - 198.

Robberecht, M., Mahall, B. E. & Nobel, P. S. (1983). Experimental removal of intra specific competitors-effects on water relations and productivity of a desert bunch grass, *Hilaria rigida*. *Oecologia* **60:** 21 - 24.

Roberts, J. (1993). Regeneration and growth of coolibah, *Eucalyptus coolabah* subsp. *arida*, a riparian tree, in the Cooper Creek region of South Australia. *Australian Journal of Ecology* **18**: 345 - 350.

Roberts, R. C. (1950). Chemical effects of salt-tolerant shrubs on soils. *Fourth International Congress of Soil Science* **1:** 404 - 406.

Roberts, B. R. & Silcock. R. G. (1993). **Western Grasses** - A grazier's guide to the grasses of South West Queensland. University of Southern Queensland Toowoomba, Queensland. pp- 141.

Roger, R. C., Haidane, R., Biard, J. F. & Boukef, K. (1986). Determination of phenolic compounds in palm (*Phoenix dactilifera*) products, date and sap extract ("legmi"). *Bulletin of Liaison-Groupe Polyphenols* **13:** 494 - 496.

Ross, M. N. & Harper, J. L. (1972). Occupation of biological space during seedling establishment. *Journal of Ecology* **60:** 77 - 88.

Russell, J. S., Moore, A. W. & Coaldrake, J. E. (1967). Relationships between subtropical, semiarid forest of *Acacia harpophylla* (Brigalow), microrelief, and chemical properties of associated gilgai soil. *Australian Journal of Botany* **15:** 481 - 498.

Sakai K. (1957). Studies on competition in plants. VII Effects on competition of a varying number of competing and non-competing individuals. *Journal of Genetics* **55:** 227 - 234.

Sands, R. & Mulligan, D. R. (1990). Water and nutrient dynamics and tree growth. *Forest Ecology and Management* **30:** 91 - 111.

Scholander, P. F., Hammel, H. T., Hemmingsen, E. A. & Bradstreet, E. D. (1965). Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. *Proceedings of the National Academy of Science of the USA* **52:** 119 - 125.

Scholes, R. J. (1990). The influence of soil fertility on the ecology of African savannas. *Journal of Biogeography* **17:** 417 - 419.

Scholes, R. J. & Archer, S. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28:** 517 - 544.

Schott, M. R. & Pieper, R. D. (1985). Influence of canopy characteristics of one-seeded juniper on understorey grasses. *Journal of Range Management* **38:** 328 - 331.

Scott, M. L., Auble, G. T. & Friedman, J. M. (1997). Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. *Ecological Applications* **7:** 677 - 690.

Searle, P. L. (1984). The Berthelot or indophenol reaction and its use in the analytical chemistry of nitrogen. *Analyst* **109**: 549-583.

Sena Gomes, A. R. & Kozlowski, T. T. (1980a). Effects of flooding on *Eucalyptus camaldulensis* and *Eucalyptus globulus* seedlings. *Oecologia* (Berlin) **46**: 139-142.

Sena Gomes, A. R. & Kozlowski. T. T. (1980b). Growth response and adaptations of *Fraxinus pennsylvanica* seedlings to flooding. *Plant Physiology* **66:** 267 - 271.

Shilling, D. G., Dusky, J. A., Mossler, M. A. & Bewick, T. A. (1992). Allelopathic potential of celery residue on lettuce. *Journal of American Society for Horticultural Science* **117:** 308 - 312.

Shinozaki, K. & Kira, T. (1956). Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. *Journal of the Institute of Polytechnics,* Osaka City University **7:** 35 - 72.

Silcock, R. G. (1973). Germination responses of native plant seeds to rainfall in south-west Queensland. *Tropical Grassland* **7:** 99 - 104.

Singh, D., Kohli, R. K. & Saxena, D. B. (1991). Effect of eucalyptus oil on germination and growth of *Phaseolus aureus* Roxb. *Plant and Soil Science* **137:** 223 - 227.

Smith, Kevin. (1998). Bureau of Meteorology. Perth. WA.

Smith, S. D. & Stubbendieck, J. (1990). Production of tall-grass prairie herbs below eastern red cedar. *Prairie Nature* **22:** 13 - 18.

Stoneman, G. L. (1992). Factors affecting the establishment of Jarrah (*Eucalyptus marginata*) from seed in the Northern Jarrah Forest of Western Australia. Ph. D. Thesis. Murdoch University, Perth. Australia.

Stoneman, G. L. & Dell, B. (1993). Growth of *Eucalyptus marginata* (jarrah) seedlings in a greenhouse in response to shade and soil temperature. *Tree Physiology* **13:** 239 - 252.

Stoneman, G. L. & Dell, B. (1994). Emergence of *Eucalyptus marginata* (jarrah) from seed in Mediterranean- climate forest in response to overstory site, seedbed and seed harvesting. *Australian Journal of Ecology* **19:** 96 - 102.

Story, R. (1967). Pasture patterns and associated soil water in partially cleared woodland. *Australian Journal of Botany* **15:** 175 - 187.

Sun, O. J., Sweet, G. B., Whitehead, D. & Graeme, D. (1995). Physiological response to water stress and waterlogging in *Nothofagus* species. *Tree Physiology* **15:** 629 - 638.

Tang, Z. C. & Kozlowski, T. T. (1982). Physiological, morphological and growth responses of *Platanus occidentalis* seedlings to flooding. *Plant and Soil* **6:** 243 - 255.

Taylor, K. M. & Aarssen, L. W. (1989). Neighbour effects in mast year seedlings of *Acer saccharum. American Journal of Botany* **76:** 546 - 554.

Thorne, A. M. & Tyler, I. M. (1997). Explanatory notes on the Roy Hill 1: 250 000, geological sheet, Western Australia, Second edition (Sheet SF50-12 international index). Geological Survey of Western Australia, Perth. pp 22.

Tian, G & Kang, B. T. (1994). Evaluation of phytotoxic effects of *Gliricidia sepium* (Jacq.) Walp pruning on maize and cowpea seedlings. *Agroforestry Systems* **26:** 249-254.

Tiedemann, A. R. & Klemmedson, J. O. (1973). Nutrient availability in desert grassland soils under mesquite (*Prosopis juliflora*) trees and adjacent open areas. *Proceedings Soil Science Society of America* **37:** 107 - 111.

Tiedemann, A. R. & Klemmedson, J. O. (1977). Effect of mesquite trees on vegetation and soils in the desert grassland. *Journal of Range Management* **30**: 361 - 367.

Tilman, R. F. (1982). Resources competition and community structure. Monographs in Population Biology Number 17. Princeton University Press. Princeton, New Jersey. pp. 296.

Tsukahara, H. & Kozlowski, T. T. (1985). Importance of adventitious roots to growth of flooded *Platanus occidentalis* seedlings. *Plant and Soil* **88:** 123 - 132.

Van Auken, O. W. & Bush, J. K. (1988). Competition between *Schizachyrium scoparium* and *Prosopis glandulosa. American Journal of Botany* **75:** 512 - 516.

van der Moezel, P. G. & Bell, D. T. (1990). Saltland reclamation: selection of superior Australian tree genotypes for discharge sites. *Proceedings of the Ecological Society of Australia* **16:** 545 - 549.

Walker, J., Robertson, J. A., Penridge, L. K. & Sharpe, P. J. H. (1986). Herbage response to tree thinning in a *Eucalyptus crebra* woodland. *Australian Journal of Ecology* **11:** 135 - 140.

Walkley, A. & Black, I. A. (1934). An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Science* **37**: 29 - 38.

Waller, G. R. (1993). Allelopathic activity of root saponins from alfalfa (*Medicago sativa* L.) on weed and wheat. *Botanical Bulletin of Academica Sinica* **34:** 1 - 11.

Wellington, A. B. (1984). Leaf water potential, fire and the regeneration of eucalypts in semi-arid, south-eastern Australia. *Oecologia* **64:** 360 - 362.

Wellington, A. B. & Noble, I. R. (1985a). Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. *Journal of Ecology* **73:** 645 - 656.

Wellington, A. B. & Noble, I. R. (1985b) Seed dynamics and factors limiting recruitment of the mallee *Eucalyptus incrassata* in semi-arid south-eastern Australia. *Journal of Ecology* **73:** 657 - 666.

Weltzin, J. K. & Coughenour, M. B. (1990). Savanna tree influence on understory vegetation and soil nutrients in north-western Kenya. *Journal of Vegetation Science* **1**: 325 - 334.

West, N. E. & Klemmendson, J. O. (1978). Structural distribution of nitrogen in desert ecosystems. pp. 1 - 16. *In* West, N. E. & Skujins, J. J. (eds) **Nitrogen in Desert Ecosystems**. Dowden Hutchinson and Ross, Stroudsburg, Pennsylvania. pp. 307.

West, N. E. & Skujins, J. J. (1978). Physical inputs of nitrogen of desert ecosystems. pp. 165 - 170. *In* West, N. E. & Skujins, J. J. (eds) **Nitrogen in Desert Ecosystems**. Dowden Hutchinson and Ross, Stroudsburg, Pennsylvania. pp. 307.

West, O. (1969). Fire : its effect on the ecology of vegetation in Rhodesia, and its application in grazing management. Proceedings Veld Management Conference, Bulawayo. Government Printer, Salisbury

White, T. C. R. (1969). An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* **50:** 905 - 999.

White, T. C. R. (1984). The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* **63:** 90 - 105.

Willis, A. J. & Groves, R. H. (1991). Temperature and light effects on the germination of seven native forbs. *Australian Journal of Botany* **39:** 219 - 228.

Winkworth, R. E. (1963). Some effects of furrow spacing and depth on soil moisture in central Australia. *Journal of Rangeland Management* **16:** 138 - 142.

Withers, J. R. (1978). Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. II. The different seedling establishment of *Eucalyptus ovata* Labill. and *Casuarina littoralis* Salisn. *Australian Journal of Botany* **26:** 465 - 484.

Wong, C. C., Rahim, H. & Sharudin, M. M. A. (1985). Shade tolerance potential of some tropical forage for integration with plantations. 1. Grasses. *MARDI Research Bulletin* **13:** 225-247

Xin, H. Z., Jeanes, B. H. & Fox, J. E. D. (1996). Assessing status and trends in tropical arid grassy pastures. pp. 157-158. *In* Hunt, L. P. & Sinclair, R. (eds). Conference Papers. 9th Biennial Australian Rangeland Conference. September 24-27th, Port Augusta, South Australia. Australian Rangeland Society.

Yamamoto, F. & Kozlowski, T. T. (1987a). Effect of flooding, tilting of stems and ethrel applications on growth, stem anatomy and ethylene production in *Pinus densiflora* seedlings. *Journal of Experimental Botany* **38:** 293 - 310.

Yamamoto, F. & Kozlowski, T. T. (1987b). Effect of flooding of soil on growth, stem anatomy and ethylene production of *Cryptomeria japonica* seedlings. *Scandinavian Journal of Forest Research* **2:** 45 - 58.

Yamamoto, F., Kozlowski, T. T. & Wolter, K. E. (1987). Effect of flooding on growth, stem and ethylene production of *Pinus halepensis* seedlings. *Canadian Journal of Forest Research* **17:** 69 - 79.

Yamamoto, F., Sakata, T. & Terazawa, K. (1995). Growth, morphology, stem anatomy and ethylene production in flooded *Alnus japonica* seedlings. *IAWA Journal* **16:** 47 - 59.

Yates, C. J. (1995). Factors limiting the recruitment of *Eucalyptus salmonophloia* F. Muell. (Salmon gum). Ph. D. thesis, Murdoch University, Western Australia. pp. 137.

Zhang, Q. (1993). Potential role of allelopathy in the soil and the decomposing root of Chinese-fir replant woodland. *Plant and Soil* **151:** 205 - 210.

Zimmermann, P. W. & Hitchcock, A. E. (1933). Initiation and stimulation of adventitious roots caused by unsaturated hydrocarbon gases. *Contribution of Boyce Thompson Institute* **5:** 351 - 369.

Appendix 1

Cyclone number	Cyclone name	Date	Lat	Long	Pressure	Category	Distance
144		02.03.'41	20.9	119.9	965	3	224
147		06.01.'42	24.0	121.5	994	1	183
150		14.02.'42	21.5	121.3	990	1	194
153		26.03.'42	23.7	121.2	995	1	138
169		08.03.'45	21.4	121.0	995	1	187
191		30.12.'47	22.1	119.6	985	2	106
196		11.03.'48	22.0	119.6	998	1	134
233		22.04.'53	21.7	121.0	1003	1	158
240		12.01.'55	21.0	121.3	980	2	241
245		18.11.'55	21.5	121.8	1003	1	229
268		21.01.'58	24.5	119.5	998	1	191
270		05.03.'58	24.5	119.3	999	1	199
271		16.03.'58	24.3	119.6	998	1	166
347	Amanda	01.01.'66	21.2	120.4	998	1	190
394	Sheilasophie	04.02.'71	24.0	118.2	990	1	235
420	Kerry	22.01.'73	23.5	119.3	980	2	111
483	Leo	27.03.'77	21.4	120.5	993	1	170
487	Vern	03.02.'78	23.6	121.0	997	1	115
506	Amy	10.01.'80	21.1	118.4	974	2	271
509	Dean	02.02.'80	24.0	121.0	989	1	149
510	Enid	17.02.'80	21.8	119.9	975	2	125
527	Rosa	03.03.'79	21.1	118.6	1000	1	257
532	Jane	09.01.'83	21.7	121.7	962	3	206
534	Lena	08.04.'83	21.7	120.8	986	1	148
732	Emma	13.12.'84	21.9	119.8	998	1	118
733	Frank	27.12.'84	21.4	119.9	997	1	169
759	Connie	20.01.'87	22.3	118.4	977	2	194
761	Elsie	26.02.'87	22.4	121.6	980	2	157
831	Annette	18.12.'94	21.2	121.8	975	2	253
845	Gertie	20.12.'95	20.9	121.9	975	2	285
849	Kirsty	12.03.'96	24.0	120.2	995	1	122
856	Rachel	08.01.'97	23.3	119.0	993	1	128

Appendix 2

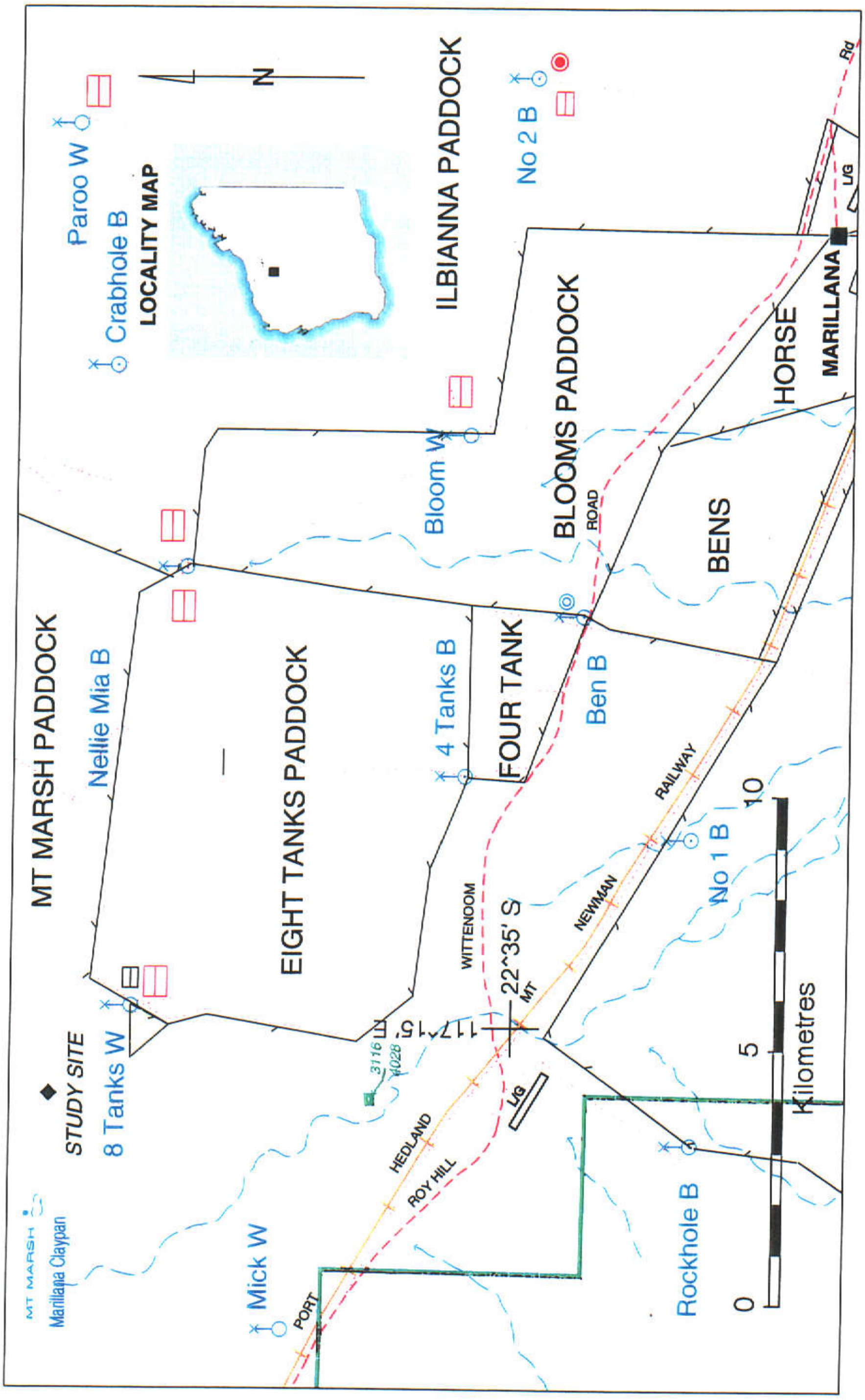

Figure details: Location of sampling sites of *E. victrix* trees, Marillana - (site 6), located just above the 8 Tanks Well. Marillana homestead shown by closed square. Black lines are tracks, green lines are boundary of stations. Thin blue lines are direction of water flow.

Appendix 3

Table 1: Samples of seed plus chaff from a bulk collection of *E. victrix*

Col 1	Col 2	Col 3	Col 4	Col 5	Col 6	Col 7	Col 8
Sample	Σ of chaff & seed mass (mg)	No. of seeds	Chaff mass (mg)	Seed mass (mg)	Seed g^{-1} of Σ chaff + seed mass	mean seed mass (mg)	% of seed in sample
1	211.1	170	89.1	122.0	805.3	0.7176	57.79
2	408.6	249	243.4	165.2	609.4	0.6635	40.43
3	291.0	157	194.5	96.5	539.5	0.6146	33.16
4	245.7	167	135.2	110.5	679.7	0.6617	44.97
5	217.5	168	118.5	99.0	772.4	0.5893	45.52
6	296.3	259	141.0	155.3	874.1	0.5996	52.41
7	220.1	186	102.2	117.9	845.1	0.6339	53.57
8	210.3	151	119.1	91.2	718.0	0.6040	43.37
Σ	2100.6	1507	1143.0	957.6	5843.5	5.0842	371.22
Mean	262.58	188.4	142.88	119.7	730.4	0.636	46.40
SD	68.42	41.9	51.46	27.3	116.5	0.043	7.93
SE	24.19	14.8	18.20	9.6	41.2	0.015	2.80

Table 2: Statistics of 8 random samples of numbers of seed g^{-1} from a bulk collection of *E. victrix*.

Item to be entered	**formula**	**Numbers of seeds g^{-1}**
Sum of observations	Σy =	5843.53
Number of observations	n =	8
Mean $\Sigma y / n$	y~ =	730.44
Squared sum	$(\Sigma y)^2$ =	34,146,877.92
Sums of squared observations	Σy^2 =	4,363,340.85
Less correction for mean	$(\Sigma y)^2 / n$ =	4,268,359.74
to give sum of squares	SSy =	94,981.11
Degrees of freedom : n-1	df =	7
Variance of observations : SSy / df	Vy =	13,568.73
Standard deviation : sq rtVy	SDy =	116.48
Coeffici't of variation %; 100 x SDy / y	CV% =	15.95

Sampling % expressed as proportion	f =	.01
Unsampled residue :1 - f	u =	.99
Variance of mean :u x Vy / n	Vy~ =	1679.13
Standard error of mean:sq rt Vy	SE y~ =	40.98
Students' t at P 0.05 (or appropriate)	t =	2.365
Confidence range : +/- t x SEy	C =	96.91
Confidence limits around the mean Upper :	y~ + C =	827.35
Lower :	y~ - C =	633.53
Sampling error % 100 x C / y	e % =	12.94

That is, there is a 95 % chance that 1.00 g of *E. victrix* seed (*i. e.* seeds + chaff, uncleaned) will contain 633 - 827 seeds.

To determine the number of samples required to meet an estimated sampling error %, then continue as follows. For a given sampling error (e%), *e. g.* if required sampling error = 10%

Then no. of samples required =

$$\left[\frac{CV\% \times t}{e\,\%} \right]^2 = 14$$

and for a range of other sampling errors :-

Required %	1	2.5	5	7.5	10	12.5	15
No. of samples	1422	228	57	25	14	9	6